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How fast do marine invertebrates burrow?

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ABSTRACT

The burrowing of bivalves, arthropods, and echinoderms collected from tidal flats and shallow subtidal sediments of the Ogeechee estuary, Georgia, U.S.A was analyzed using time-elapse, X-ray analysis of thin-walled aquaria. The rate of sediment intrusion was determined for each animal. Burrowing rates ranged between 0.01 and 0.15 cm^3/h for suspension-feeding animals. Deposit-feeding animals moved between 1 and 10 cm^3 of sand per hour, approximately 10 to 100 times more sediment than the suspension feeders moved over similar times.

Neoichnological experiments show that ten filter-feeding individuals could take as long as 115 yr to churn a 1 m^2 plot of sediment, by indexing the measured burrowing rates to realistic animal population densities. Ten such mobile deposit feeders as irregular echinoderms could bioturbate the same sediment in just 42 days. Under the maximum population densities modeled, the animals could bioturbate the sediment plot in 61 min. Given the reported results, qualitative interpretation of the rock record is possible: highly burrowed examples of the *Skolithos* Ichnofacies reflect high population densities and at least seasonal time spans. Highly burrowed examples of the *Cruziana* Ichnofacies may represent moderate population densities and short time spans.

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1. Introduction

This study sets out to establish reasonable bioturbation rates from a range of marine animals that exhibit contrasting feeding or motility habits. Included in this study are the arthropods *Neohaustorius*, *Acanthohaustorus*, *Chiridotea caeca*, and *Lepidopa websteri*; the bivalves *Labiosa lineata*, *Macoma balthica*, *Dosinia discus*, and *Solen viridis*; and the echinoderms *Hemipholis elongata*, *Moira atropos*, and *Thyone briareus*.

Among the more interesting aspects of trace fossils is their potential to provide specific information regarding sedimentation processes and rates. Substrate-dependant ichnofacies, for example, can be used to infer sediment cohesiveness at the time of burrow emplacement. Such equilibrichnia structures as *Diplocraterion yoyo* (Goldring) can be used to suggest aggradation or degradation of the sedimentary surface during animal colonization. And sedimentation rates have been inferred by wholesale readjustment of biogenic structures, which is especially common with *Rosselia socialis* Dahmer (Nara, 1997) and *Conichnus* Myannil (Savrda, 2002). Despite the aforementioned efforts towards establishing a process-based ichnology, the field is hampered by a lack of data directly pertaining to the rate at which burrows are emplaced (Signor, 1982; Alexander et al., 1993; Dashtgard and Gingras, 2005; Dafoe et al., 2008). If time constraints were better understood, realistic estimates could be made for the duration of colonization or bioturbation events. In fact, the approximate time represented by various classes of bioturbate textures could be deduced (Taylor et al., 2003).

2. Methods

The Ogeechee estuary is immediately south of Savannah, GA (USA: 31° 50′46″N, 81° 04′36″W). Adult animals collected from tidal flats and shallow subtidal sediments of the Ogeechee estuary included *Neohaustorius*, *Acanthohaustorus*, *Chiridotea caeca*, *Lepidopa websteri*, *Labiosa lineata*, *Macoma balthica*, *Doscinia discus*, *Solen viridis*, *Hemipholis elongata*, *Moira atropos*, and *Thyone briareus*. All of the invertebrates were sustained in marine aquaria that circulated the estuary's waters. Quartz-rich sediment in the aquaria was taken from the same locale from which the animals were sampled. Heavy minerals used to emphasize lamination in the X-ray plates were manually taken from beach placers at various locales. Temperature, salinity, and food were maintained with the consistent introduction of new water.

Thin-walled aquaria were constructed from glass. To accommodate the different sizes of animals, the dimensions of the aquaria were variable, ranging from 20×20 cm to 35×25 cm and 1.5 to 2.5 cm wide. Aquaria were filled with laminated fine-grained sand. Laminations

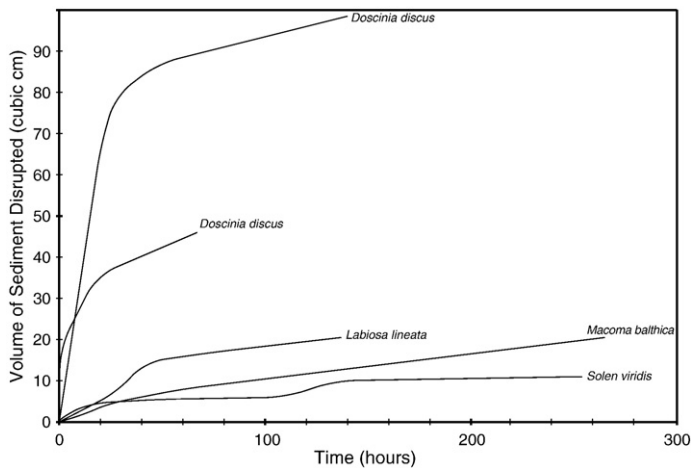**Fig. 1.** Volume of sediment disrupted (cm³) versus time (h) for the bivalves *Doscinia discus* (two experiments shown), *Labiosa lineata*, *Macoma balthica*, and *Solen viridis*.
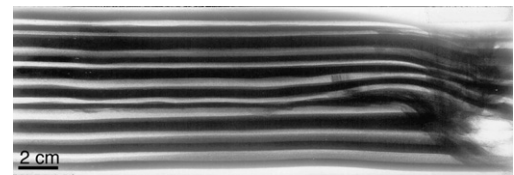

Fig. 3. *Labiosa lineata* after 24 h. Field of view is 24 cm wide.

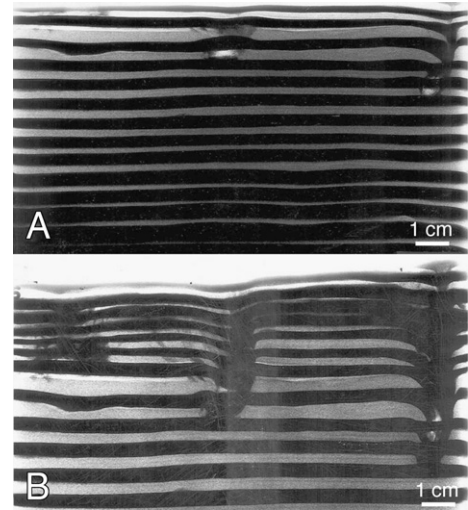**Fig. 4.** The movement of *Macoma balthica* in the thin-walled aquaria at various time steps. A. 1 h. B. 24 h. Field of view is 14 cm wide.

were made evenly by filling the aquaria with water and sprinkling sand by hand into the water. Quartz sand was interbedded with heavy mineral sand dominantly comprised magnetite to facilitate visual and density contrasts. The bedding thicknesses were variable: each layer was 5–10 mm thick.

The thin-walled aquaria were placed in estuary–water tanks so that the entire aquaria were completely immersed in water. Thereafter, the aquaria were selectively inoculated with one type of animal. Depending on the size and availability of the animals collected, the thin aquaria were inoculated with one to six individuals of the selected taxa. At variable time steps–about 1, 6, 24, 72, and 144 h–X-ray images were collected using a Soyee portable X-ray system (SY-31-100P). The time-stepped X-ray images were analyzed to determine the amount of sediment disruption that occurred between steps. The amount of sediment disruption was assessed in two dimensions using a digital planimeter. The two-dimensional area was converted to a volume of burrowed sediment by multiplying the area by the width of a typical burrow. Linear burrowing velocity was calculated by measuring the change in the combined length of all burrow axes between time steps. We use below the informal terms "intrusion time" and "subsequent time". The intrusion time is the time elapsed for the animal to attain their normal position (tier) within the sediment. Although subjective, this concept is useful as initial sediment intrusion rates were generally much higher than subsequent bioturbation rates. All reported burrowing rates are in cm³/h and cm/h

and are normalized per individual. Sources of error are discussed in the results, below.

3. Results

In general, animal intrusion or advection (mainly burrowing) into the sediment was initially rapid with the rate of sediment reworking decreasing with time. Sediment displacement during initial intrusion for filter-feeding and interface deposit-feeding animals was as much as 100 times more rapid than the steady state sediment dwelling phase. Initial burrowing rates for sediment-swimming and sediment-advective behaviors were generally only 10 times more rapid than the subsequent sediment reworking.
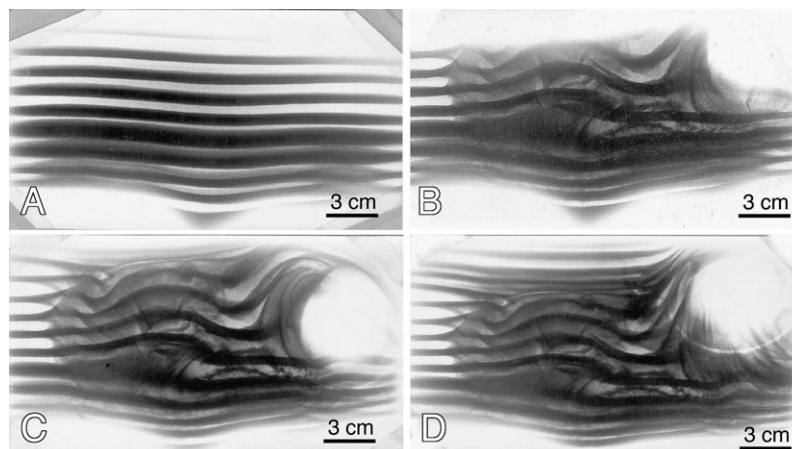

Fig. 2. The movement of *Doscinia discus* in the thin-walled aquaria at various time steps. A. 1 h. B. 6 h. C. 12 h. D. 24 h. Field of view is 24 cm wide.
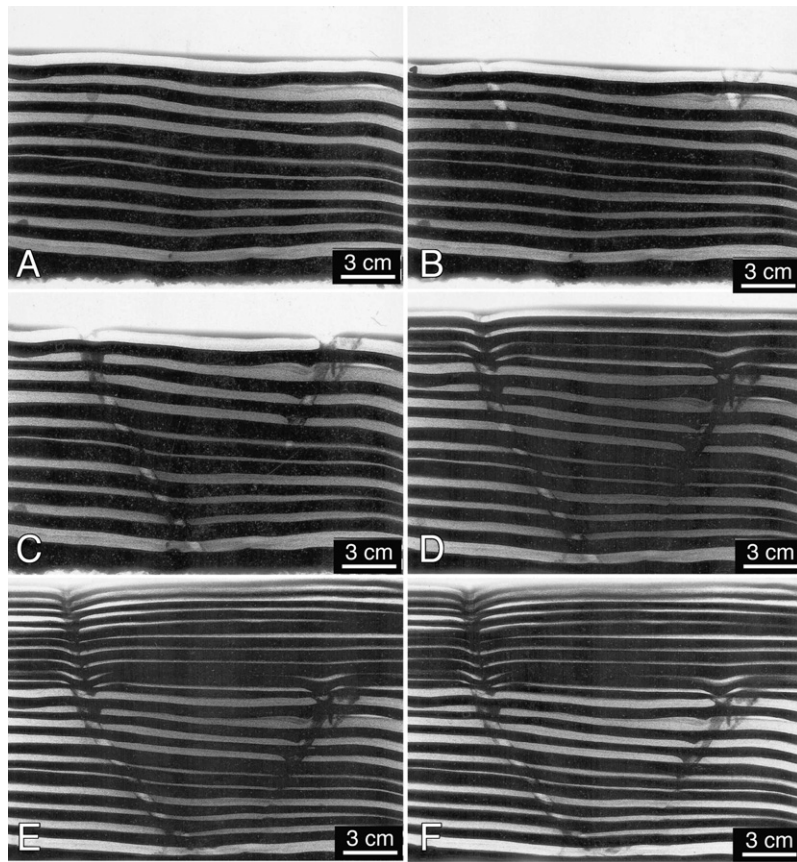
Fig. 5. _Solen viridis_ at different time steps. A. 1 h. B. 6 h. C. 12 h. D. 24 h. E. 48 h. F. 72 h. Field of view is 24 cm wide.

For individual animals, size proved to be the most important parameter relating to volumetric sediment displacement. Larger animals displaced more sediment more rapidly than smaller animals. Linear burrow velocity, however, was indicative of behavioral and physiological adaptations and was highly variable between all animals.

3.1. Bivalves

Bivalves showed a broad range in volumetric sediment displacement and burrowing velocity. _Dosinia discus_ moved 7–10 cm^3 of sand per hour during the first 10 h following inoculation into the aquaria (Figs. 1 and 2). This fell well below 1 cm^3/h after 24 h in the aquaria.
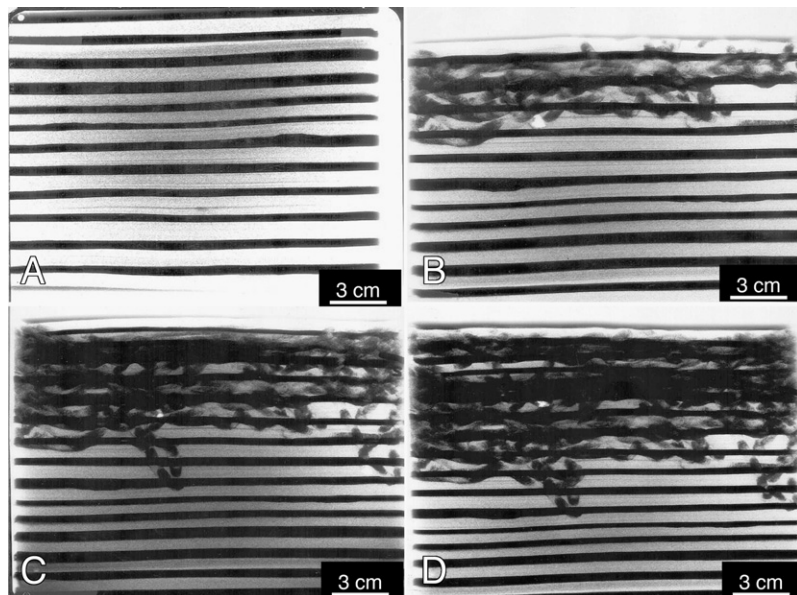

Fig. 6. _Lepidopa websteri_ at different time steps. A. 1 h. B. 6 h. C. 12 h. D. 24 h. Field of view is 24 cm wide.
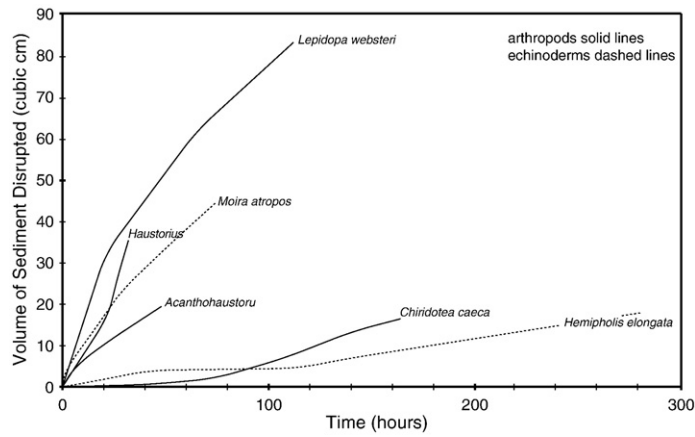
Fig. 7. Volume of sediment disrupted (cm³) versus time (h) for the arthropods and echinoderms in this study: *Neohaustorius, Acanthohaustorus, Chiridotea caeca, Lepidopa websteri, Hemipholis elongata*, and *Moira atropos. Thyone briareus* not shown.

Dosinia was also the fastest burrower of the study. It attained linear velocities of 29 cm/h outpacing all of the other animals by at least one order of magnitude.

Bivalves *Labiosa lineata, Macoma balthica*, and *Solen viridis* (Figs. 3–5, respectively) displaced sediment more slowly: generally 0.5 cm³/h for the first 10–24 h and leveling off to 0.1 to 0.01 cm³/h after 24 h in the aquaria (Fig. 1). Linear burrow velocities were variable. *Solen viridis* achieved velocities as high as 2.1 cm/h, whereas *Labiosa lineata* and *Macoma balthica* moved at 0.1 to 0.6 cm/h (Table 1).

3.2. Arthropods

Arthropods studied differed from the bivalves in that they burrowed more consistently and their activities remained steady over time. *Lepidopa websteri*, the mole crab (Fig. 6), was the most active burrower observed in this group. An individual could consistently displace 2 cm³/h and maintain linear velocities between 3 and 6 cm/h. Individual *Haustorius* and *Acanthohaustorus* displaced 0.5 to 0.7 cm³/h (Figs. 7–9). *Haustorius* moved as rapidly as 5 cm/h, whereas *Acanthohaustorus* normally traveled at 1 cm/h. *Chiridotea* was the only animal in the experiment that demonstrated a low initial sediment advection rate with a later increase in burrowing activity (Figs. 7, 10). For the first 24 h, almost no burrowing was detected for *Chiridotea*. Subsequently, individuals started to burrow at 0.2 cm³/h and continued to do so until the end of the experiment.

3.3. Echinoderms

Echinoderms used in this experiment showed a broad range of burrowing behaviors. *Moira atropos*, an irregular echinoderm, was a fast and effective burrower (Fig. 11). It moved about 5 cm³/h and traveled at speeds as high as 2 cm/h. This is in contrast with the other echinoderms tested, such as the brittle star *Hemipholis elongata*, which displaced only 0.05 cm³/h and moved through sediment with a velocity of approximately 0.05 to 0.08 cm/h (Fig. 12). The sea cucumber, *Thyone briareus*, was also tested with this group. It could
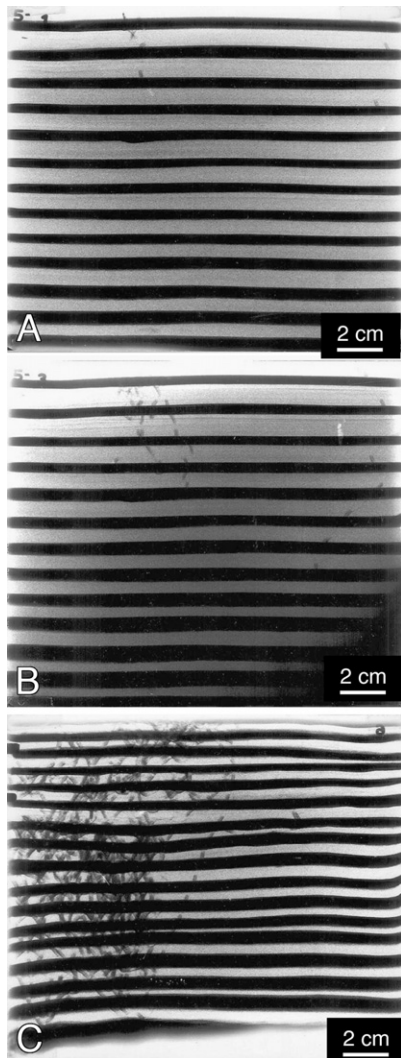

Fig. 8. *Neohaustorius* at different time steps. A. 1 h. B. 6 h. C. 24 h. Field of view is 18 cm wide.
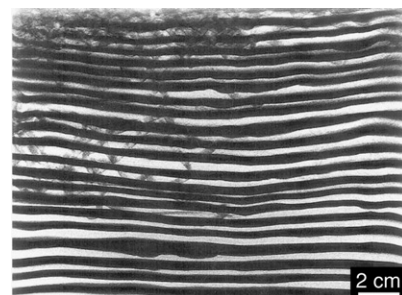

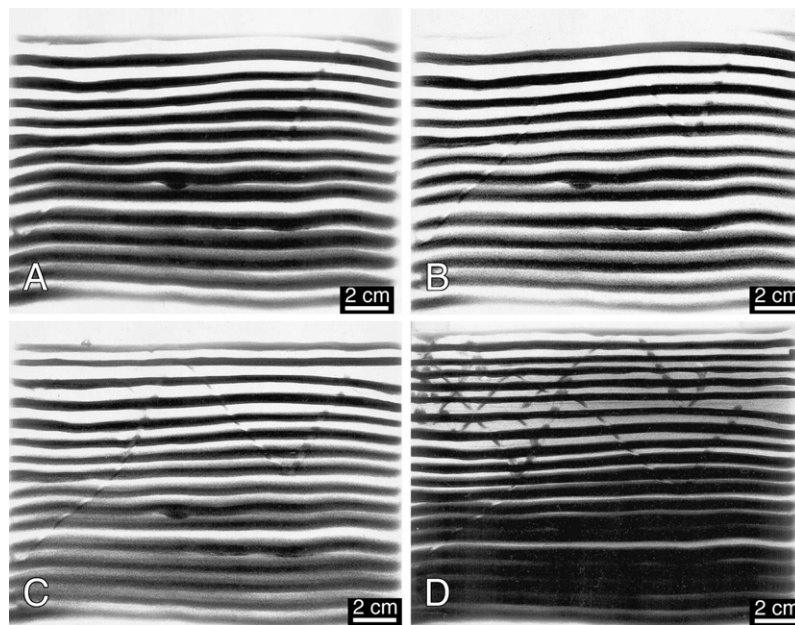**Fig. 9.** *Acanthohaustorus* after 24 h. Field of view is 20 cm wide.

Fig. 10. *Chiridotea caeca* shown at incremental time steps. A. 1 h. B. 12 h. C. 24 h. D. 48 h. Field of view is 18 cm wide.

not be encouraged to burrow in the aquarium, however, even though it was collected from a U-shaped burrow in the tidal flats.

3.4. Sources of error

Measurements with the planimeter were tested for error using drafted 100 cm^2 plots. The error therein was 2–4% on ten tests. This error is likely small compared to the error introduced during volumetric calculation of burrowing, which required that the cross-sectional area of the burrow be approximated by considering the cross-sectional size of the animal. This introduces about 10% error, which is only estimated because of experimental constraints. Linear burrowing velocities are the most accurate data reported: the measurements reveal the linear or curvilinear propagation of the burrow centerline. With the smaller animals, some movement in and out of the plane would be undetected in the X-ray images. Although this is probably a minor consideration, we suggest that a 5% error be ascribed to burrowing velocity as well. In other words, volumetric burrowing assessments should be accurate within 14% of the reported results and burrowing velocity within 9%. It is likely that behavior and motility are influenced by population density. Although difficult to quantify, this is another source of error that needs to be considered in the context of Fig. 14. Although we do not speculate on the impact of population-density dependant sources of error, future work might focus on adding that parameter. Lastly, the animals are burrowing in decidedly unnatural conditions. In natural settings with natural stimuli, their activities might be much more rapid or slower.

4. Interpretation and discussion

It is difficult to generalize the observed data with respect to the type of organism. The bivalves, arthropods, and echinoderms present a wide range of volumetric bioturbation efficiency. If the burrowing animals are separated by primary ethology, however, the reported burrowing rates are revealing. Of the animals studied, 4 are suspension feeders or interface detritovores that feed from a fixed locale and possibly changing locations from time to time, including *Labiosa lineata*, *Macoma balthica* (Olafsson, 1986), *Solen viridis*, and *Hemipholis elongata* (McAlister and Stancyk, 2003). Five of the animals studied graze within the sediment for food or have the ability to move

rapidly to change their locale of interface feeding; these are *Dosinia discus* (Norton, 1947), *Neohaustorius* (Croker, 1967), *Acanthohaustorus* (Croker, 1967), *Lepidopa websteri* (Howard, 1968), and *Moira atropos* (Fu and Werner, 2000). *Chiridotea caeca* (McDermotta, 2005) is primarily a scavenger that lives in the upper few millimeters of the sediment.

Within these behavioral groups, the data presented is consistent (Fig. 13). Suspension-feeding animals (i.e. *Labiosa lineata*, *Macoma balthica*, *Solen viridis*, *Hemipholis elongata* shown in Fig. 13) intrude the sediment more slowly and tend to shift within the sediment only small distances: most commonly in a vertical vector. The practical
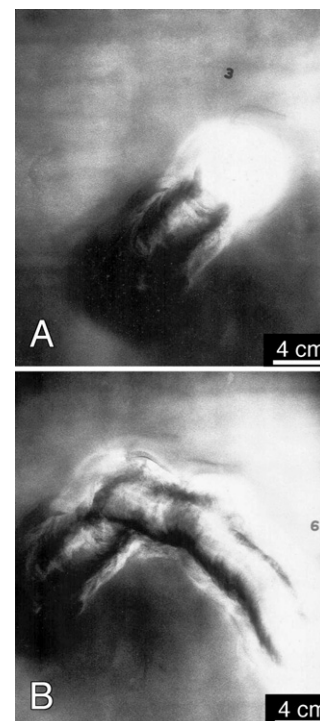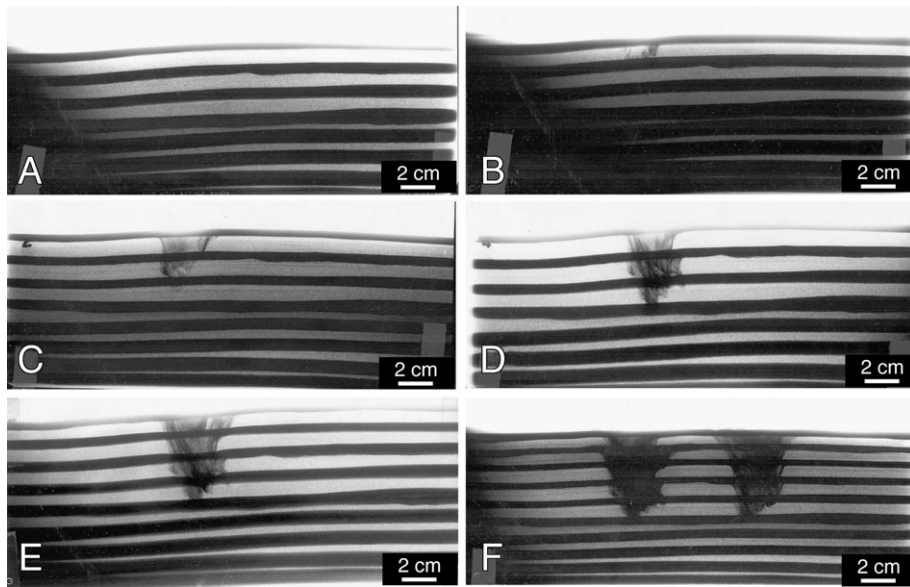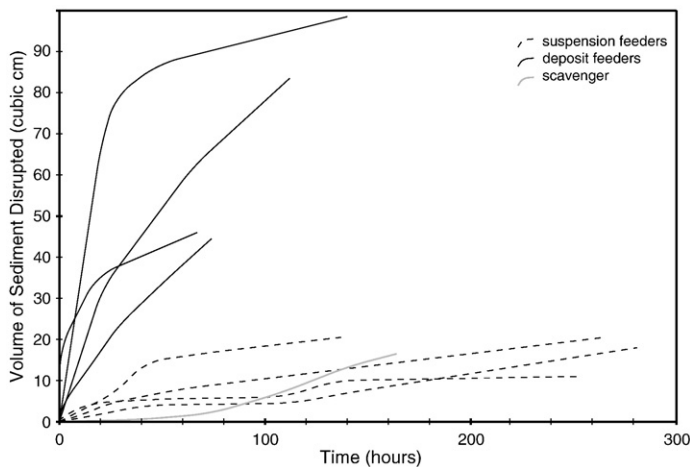

Fig. 11. *Moira atropos* shown at two time steps. View is from above so side-view laminations not visible. A. 6 h. B. 24 h. Field of view is 23 cm wide.

Fig. 12. *Hemipholis elongata* at the incremental time steps. A. Initial aquarium (*t*=0). B. 6 h. C. 12 h. D. 24 h. E. 48 h. F. 72 h showing a second brittle star added at *t*=48 to check slow burrowing rates. Field of view is 24 cm wide.

range of their volumetric burrowing rate was between 0.01 and 0.15 cm^3 of sand per hour (*Solen* and *Labiosa*, respectively) with typical linear motility of 0.1 cm/h and a maximum of 2.1 cm/h (recorded for *Solen*). Compared to the ranges for deposit feeders (below), the reported values are very low. This is a result of the suspension feeder's primarily stationary habit, a luxury more or less particular to filter feeding.

Deposit-feeding animals (i.e. *Neohaustorius*, *Acanthohaustorus*, *Lepidopa websteri*, *Dosinia discus*, shown in Fig. 13) travel through and disrupt much greater volumes of sand—generally 10 to 100 times more than the suspension feeders. Within this study, the range of volumetric burrowing rates for deposit feeders was between 1 and 10 cm^3 of sand per hour (*Ananthohaustorus* and *Dosinia*, respectively). The same animals achieved linear velocities between 1 and 30 cm/h. Naturally, rapid movement through sediment is advantageous for deposit-feeding animals. It is an energy-intensive activity, however, and may explain the tailing-off of some of the deposit-feeding animal's sediment processing over time (Table 1, Fig. 13).

The final category of animal behavior presented herein is that of *Chirodotea* (Figs. 7, 10). *Chirodotea* is a scavenger. The lack of food at the sediment–water interface drove the arthropod to use secondary behaviors to exploit secondary sources of food: this did not occur until two days had elapsed. At this point, *Chirodotea* switched to deposit feeding and its volumetric burrowing rate increased notably (0.2 cm^3/h).

Thayer (1983) provided a review of the Phanerozoic history of animal–sediment interactions. He used an actualistic approach considering extant taxa to conclude that Mesozoic and Cenozoic taxa

Fig. 13. Volume of sediment disrupted (cm^3) versus time (h) for suspension feeders, deposit feeders, and scavengers.
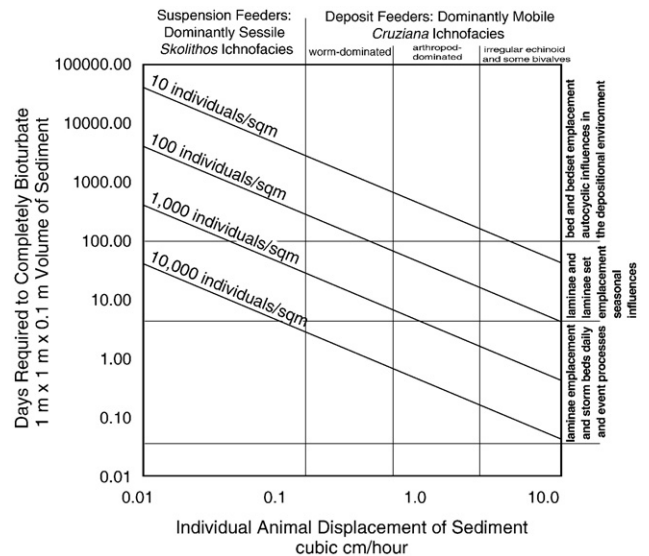
Fig. 14. Graph showing the amount of time required in days (*x*-axis) to bioturbate a volume of sediment equivalent to 1 m × 1 m × 0.1 m—or 1 m^2 of a typical depositional surface. The number of days is plotted against the rate of sediment displacement of an individual animal. The range of sediment displacement rates used are based on this study. Oblique lines across the graph represent the work of various population densities. So, if an animal can displace 1 cm^3/h of sediment, 1000 similar individuals can bioturbate the proposed volume of sediment in about 6 days. The chart is further divided into typical burrowing rates for suspension-feeding dominated ichnofacies (Skolithos) and deposit-feeding dominated ichnofacies (Cruziana). Although this is based on the limited data provided herein, it is an attractive conceptualization that shows the potential of such technology.

caused higher sediment convection rates than those of the Paleozoic. Thayer suggested that intensively bioturbating taxa were capable of reworking the sediment at a rate of 10 cm^3 per day (or more). Likewise, the results of this study can be applied conceptually to modern sedimentary environments and the rock record. The range of volumetric burrowing rates herein is 0.01 to 10.0 cm^3/h. These values are taken to be representative ranges for natural burrowing rates. In Fig. 14, those burrowing rates are indexed to various (hypothetical) population-density curves, which are represented as lines on a log–log plot. The rate of (volumetric) burrowing can be multiplied by the number of individuals to determine the time required to bioturbate a given volume of sediment; in this case a 1 m × 1 m × 0.10 m representative elemental volume (REV) of sediment. Ten individuals in the REV would take 115 yr (42,000 days) to churn the sediment where all very long-lived filter-feeding animals displace only 0.1 cm^3/h of sediment. Where these animals mobile deposit feeders, such as an irregular echinoderm, a small population of just 10 animals would be capable of churning the REV in just 42 days.

High population densities naturally churn the sediment much more rapidly. Ten thousand suspension feeders could bioturbate the proposed REV in 42 days and 10,000 deposit feeders could eradicate all physical sedimentary structure in 61 min! As stated above, the ranges for burrowing rates are at least credible based on the results of this study. The ranges for population densities are also realistic. Low densities of suspension-feeding animals are 1–10 individuals/m^2. For example, high densities of interface-feeding (fixed location) *Corophium* (a marginal-marine arthropod) commonly exceed 40,000 individuals/m^2, and *Euzonus*, a deposit-feeding opheliid polychaete is reported to reside in populations exceeding 5000 individuals/m^2 (Gingras, personal observation, 2005).

It can be inferred from the above that in the rock record, sedimentary horizons dominated by the *Skolithos* Ichnofacies comprise animal burrows that represent more ponderous construction. Thereby, highly burrowed horizons exclusively colonized by elements of the *Skolithos* Ichnofacies likely reflect very high population densities and at least seasonal time spans. In contrast, highly burrowed examples of the *Cruziana* Ichnofacies may represent moderate population densities and impressively short time spans. This would be especially true of deposits dominated by very motile examples of the *Cruziana* Ichnofacies, including *Scolicia* or some styles (bivalve-generated) of *Protovirgularia*, as these behaviors likely represent very rapid processing of the sediment. We also suspect that some arthropods, such as thalassinid shrimp, are capable of bioturbation rates even higher than the limits shown in Fig. 14. Thalassinid shrimp were not, however, included in the tested animals.

5. Conclusions

This study shows the striking range of burrowing rates that exist between morphologically similar animals that use different feeding strategies. Suspension-feeding animals intrude the sediment more slowly than deposit feeders, and exhibit a range in their volumetric burrowing rates from 0.01 and 0.15 cm^3/h. Conversely, deposit-feeding animals move 10 to 100 times more sediment than suspension feeders. The range of volumetric burrowing rates within the deposit feeders was between 1 and 10 cm^3 of sand per hour.

By indexing the measured burrowing rates to realistic but hypothetical animal population densities, we suggest that ten filter-feeding individuals would take 115 yr to churn a 1 m^2 plot of sediment. Ten such mobile deposit feeders as irregular echinoderms could churn the same sediment in just 42 days. Under high population densities, the animals could bioturbate the sediment in 61 min. These results suggest that qualitative interpretation of the rock record can be made, where highly burrowed examples of the *Skolithos* Ichnofacies reflect high population densities and at least seasonal time spans. Highly burrowed examples of the *Cruziana* Ichnofacies may represent moderate population densities and short time spans.

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