

In situ studies of megafaunal mounds indicate rapid sediment turnover and community response at the deep-sea floor

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Sediment mounds, composed of faecal material from megafaunal deposit feeders^{1,2}, occur in virtually all deep-sea environments, forming the dominant decimetre-scale topography on the ocean floor^{3,4}. Mounds are often zones of deep, convective bioturbation^{1,2}, and their formation is thought to disturb infaunal benthos^{5,6}. We are studying mounds in the deep sea to evaluate rates and patterns of megafaunal sediment mixing, and to assess the disturbance effects of mound building on the infaunal community, with the goal of using mounds to investigate natural processes of succession at the deep-sea floor⁷. Our results indicate that sediment turnover associated with mound building by echiuran worms can be very rapid, and that bathyal infauna can respond quickly to this type of disturbance. These findings suggest that spatially rare but dynamic elements in the sediment fabric, such as mounds, may be important in controlling microstratigraphy, chemical diagenesis and community structure at the deep-sea floor.

At our study site at a depth of 1,240 m in the Santa Catalina Basin⁸ (33°12' N, 118° 30' W), large mounds (~10 cm high and 30 cm in diameter) are relatively abundant, covering ~2% of the sea bed. The most common type of mound is apparently formed of faecal pellets from a large echiuran worm, probably *Prometor benthophila*⁹. The echiuran appears to feed on surface sediments in a shallow pit (~10 cm deep and ~1 m diameter)¹⁰, depositing its faeces by means of U-shaped burrows on one of several peripheral mounds⁹⁻¹².

Several lines of evidence indicate faecal deposition rates on mounds of ~1-2 cm per month, that is, rates ~1,000 times higher than those of long-term sediment accumulation in the Santa Catalina Basin (SCB)¹³. The most dramatic evidence comes from time-lapse, stereo photographs. These were obtained *in situ* from a camera tripod placed by the research submersible *Alvin* over a mound from 17 December 1984 to 4 February 1985. Photographs taken at 10-h intervals yielded sequential profiles (Fig. 1) which indicate ~1-2 cm of deposition out to a radius of 5-8 cm from the central burrow during the 120 h immediately following camera deployment. This growth episode was followed by a 30-day quiescent period, during which no appreciable deposition took place, even though the echiuran was photographed in its burrow.

Depth distributions of tracer beads spread on the surface of mounds also indicate faecal deposition rates of 1-2 cm per month. *Alvin* spread spherical glass beads (5-420 µm diameter, 2.42 g cm⁻³ specific gravity) on three steep-sided (and therefore active) mounds, and in three control areas, between 14 and 16 December 1984; the submersible returned and collected core samples on these marked sites ~50 days later. Cores were analysed for beads at 1-cm depth intervals. All three marked mounds exhibited tracer beads to depths of 1-3 cm, with peak bead abundance typically occurring in the 1-2-cm layer; in control sites, beads were essentially restricted to the top centimetre of sediment (Fig. 2). Sub-surface peaks in tracer distributions on mounds suggest that sediment deposition, rather than diffusive sediment mixing, 'moved' beads downward¹⁴, indicating mound growth rates of ≥1 cm per month. In addition, two mounds showed marked secondary bead peaks at depths of 6-8 cm (Fig. 2); this suggests transport of surface sediments

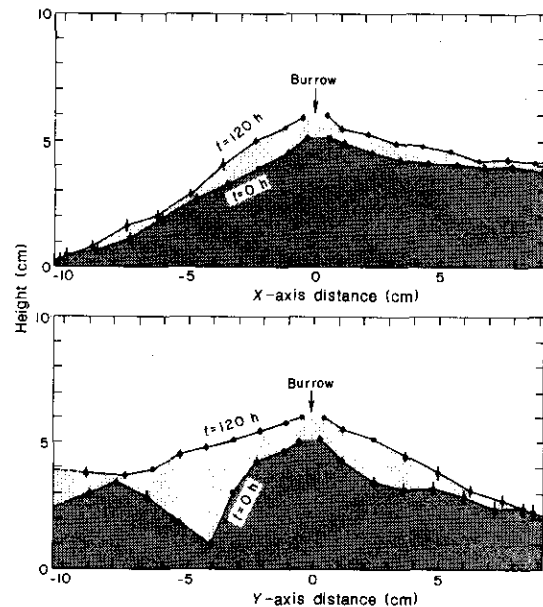


Fig. 1 Cross-sectional profiles through the peak of an echiuran mound, drawn from stereo photographs using a stereocomparator. Sets of profiles are drawn along two normal axes, from photographs taken shortly after the camera was emplaced ($t=0$ h) and 120 h later ($t=120$ h). Each point represents the mean (\pm s.e.) of five replicate runs with the stereocomparator. Heights are referenced to an arbitrary base level.

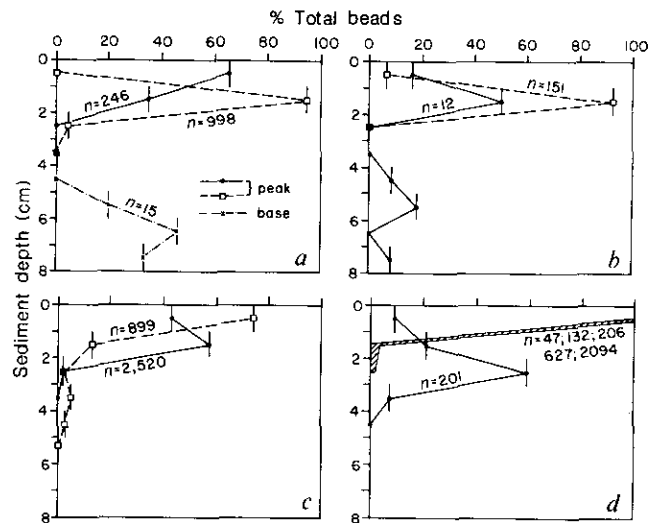


Fig. 2 Vertical distributions in the sediment of glass beads (208-420 µm diameter, that is, the approximate *in situ* grain size of pelletized SCB sediment) spread at the sediment-water interface 50 days before sampling. The number of beads in each profile is indicated (n). *a*, Vertical profiles near the peak and at the base of a mound (1510-E2); *b*, *c*, profiles near the peaks of mounds (1512-A5 and 1512-A6, respectively); *d*, profiles from background sediments (control sites). The hatched area in *d* encloses curves from five control cores. The sub-surface peak in one of the control profiles apparently results from bead penetration of an animal burrow.

Methods. Beads were spread from *Alvin* using a screen-covered dispenser. Core samples (~30 cm long) were taken 50 days later in labelled areas with 400-cm² Ekman corers or 35-cm² *Alvin* corers⁶. On board ship, these cores were subsampled for beads, using 2.2-cm-diameter syringe corers inserted to a depth of 9 cm. Syringe cores were extruded, cut off at intervals of 1 cm and preserved in formalin. Beads retained on a 208-µm sieve were subsequently counted using dark-field microscopy. Data from the 8-9-cm depth intervals of bead cores are not presented because

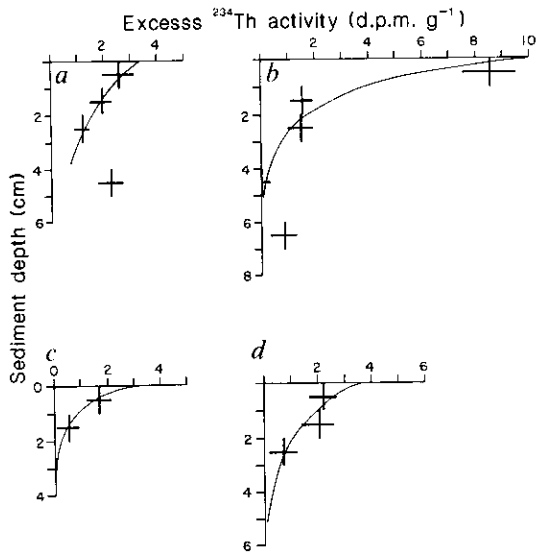


Fig. 3 Depth distributions of excess ^{234}Th activity in four active mounds. Measurements (crosses) were made over vertical intervals of 1 cm; horizontal error bars indicate ± 1 s.d. from counting statistics. Curves indicate expected distributions of ^{234}Th excess given constant surface activity and deposition rates (w), and assuming minimal sediment mixing¹⁶. a, Mound 1491, $w = 2.2$ cm per month; b, mound 1499, $w = 1.0$; c, mound 1500-1, $w = 0.7$; d, mound 1500-2, $w = 1.4$.

Methods. ^{234}Th measurements were made on 35-cm² core samples collected from mounds using *Alvin*. On board ship, cores were extruded and sectioned at 1-cm intervals; the outside 'rind' (~ 2 mm) of each sampled interval was discarded to avoid contamination resulting from core insertion. Samples were counted using the methods of ref. 16.

mixing depth associated with mounds.

Depth distributions of excess ^{234}Th on four mounds also suggest rapid, episodic deposition. ^{234}Th , a decay product of ^{238}U with a 24-day half-life, is produced in the water column and scavenged by sinking particles¹⁵. The excess ^{234}Th signal picked up by particles during transit through the water column remains detectable in bottom sediments for ~ 100 days¹⁶. *Alvin* collected core samples on four apparently active mounds on 28 November and 14–15 December 1984; these cores were horizontally sectioned and analysed for excess ^{234}Th . Vertical profiles from the mounds (Fig. 3) show excess ^{234}Th to depths of 2–3 cm (excluding sub-surface peaks from burrow 'piping'¹⁷). Two profiles (1499 and 1500-2) also show nearly constant ^{234}Th excess within vertical depth intervals of 2 cm (Fig. 3); we interpret these as representing episodes of faecal production, during which 1–2 cm of sediment was rapidly deposited on top of the mound. Assuming relatively constant ^{234}Th activity (over time) in surface sediments consumed by echiurans, an advection model for sediment accumulation¹⁶ yields mound deposition rates (w) of ~ 1 –2 cm per month (Fig. 3). The deposition rates determined from the model represent upper limits, because diffusive mixing may contribute to the penetration depth of the excess ^{234}Th signal. X-radiographs of mound sediments cored by *Alvin* reveal few bioturbation structures, however, suggesting that diffusive sediment mixing is unlikely to have significantly affected the penetration of excess ^{234}Th into mound sediments.

The high deposition rates on mounds can be viewed in a basin-wide context by roughly calculating the population-level reworking rates of the echiurans. A photo-sled survey¹⁸ made on 23 November 1984 indicates active (steep-sided) mound densities of ~ 0.14 m⁻²; if the mounds are 10 cm high, 30 cm wide, and are covered by 1 cm of new faecal material per month, echiurans are processing sediment at the rate of $\sim 1,500$ ml m⁻² yr⁻¹. Thus, the top 10 cm of sediment in the SCB can be turned over by echiurans in ~ 70 yr: or, in other words, a sediment

particle will, on average, pass through an echiuran gut ~ 10 times before permanent burial¹³. Consequently, while echiuran mounds are rare enough to be poorly sampled by corers from surface vessels, they are likely to have dramatic effects on sediment mixing depths and diagenetic processes at the SCB floor^{14,19}.

The high deposition rates on mounds seem likely to cause major disturbances of the sediment-dwelling community. Deposition rates of 1–2 cm per month cause significant disturbance of intertidal benthos, especially if sediment accumulation is episodic^{20,21}; it seems reasonable that infauna from low-energy, deep-sea environments should be at least as sensitive²². To assess the effect of an episode of mound building on the SCB infauna, we created artificial mounds devoid of macrofauna. This was done by placing recently obtained sub-surface basin sediment into a conical mould; *Alvin* was then used to deposit these sediment cones (~ 10 cm high and 45 cm in diameter) on the sea floor on 15–16 December 1984. *Alvin* returned ~ 50 days later and collected core samples for macrofauna on two artificial structures, and from the surrounding, level sea floor (Fig. 4). We collected core samples from portions of the artificial mounds that were 4–10 cm in height; that is, from areas where the original seafloor community was buried to depths of 4–10 cm.

Macrofaunal abundance and species richness on artificial mounds in place for 50 days were unexpectedly high, attaining levels 52–85% of those in background community samples (Fig. 4). The species composition of mound samples was also surprisingly similar to those from the background community; >95% of the animals collected on mounds belonged to species present in background community samples. In addition, the three most abundant species in artificial mounds were among the four most abundant in background samples; in each case

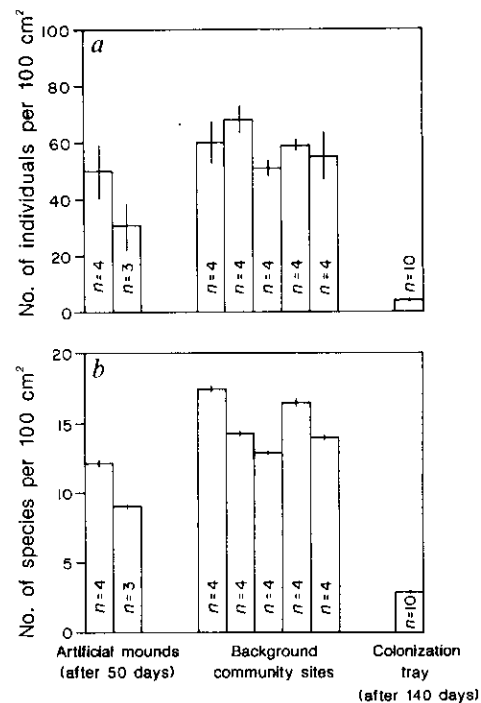


Fig. 4 Mean (\pm s.e.) abundance (a) and species richness (b) of macrofauna (>420 μm) from replicate 100-cm² core samples (n = number of samples) collected from two artificial mounds (left), five locations in the background community ≥ 70 cm from the nearest mound (middle), and a colonization tray of pre-frozen sediment placed on the sea floor for 140 days²⁷ (right).

Methods. Cores sampled 100 cm² of sediment surface area to a depth of 10 cm. Samples from artificial mounds and the background community were collected using *Alvin* and processed as in ref. 6. Colonization-tray data are from ref. 27.

Table 1 Species contributing $\geq 1.9\%$ of the individuals in two sets of artificial mound cores, and five sets of background community cores

Artificial mounds ($n = 2$)		Background sites ($n = 5$)	
<i>Levinsenia oculata</i>	$68 \pm 2\%*$	<i>Levinsenia oculata</i>	$67 \pm 1\%$
<i>Tharyx monilaris</i>	$5.4 \pm 3.4\%$	<i>Tharyx tessellata</i>	$3.9 \pm 0.5\%$
<i>Cossura</i> sp.	$5.1 \pm 1.8\%$	<i>Cossura</i> sp.	$3.2 \pm 0.7\%$
Tanaid sp.	$1.9 \pm 0.4\%$	<i>Tharyx monilaris</i>	$2.0 \pm 0.5\%$

* Mean \pm standard error.

these three species accounted for $>72\%$ of total macrofaunal abundance (Table 1).

There are two reasonable explanations for the abundance of macrofauna in artificial mounds after 50 days. The first is that the normal SCB assemblage is resistant to burial, with many of its species able to burrow upward through 4–10 cm of rapidly deposited sediment. If this is true, these deep-sea organisms seem better able to withstand burial than many shallow-water species from more physically active environments^{20,21,23,24}. Alternatively, the presence of macrofauna in artificial mounds may result from colonization, arising through immigration from

surrounding sediments or recruitment from the water column. If colonization is responsible, the implied rates of community recovery are at least an order of magnitude faster than obtained in earlier deep-sea studies of colonization^{25–27} (Fig. 4). Such differences in colonization rate could well result from biases introduced by the design of earlier experiments, which isolated sediments from the surrounding sea floor in elevated trays^{6,7}.

Whether explained by upward burrowing or by colonization, the abundance of macrofauna in artificial mounds indicates an unexpectedly rapid response in a deep-sea community²². Many SCB species are thus adapted to respond to frequent disturbance resulting from echinuran mound building. In view of the widespread occurrence of echinurans^{9,12} and other mound builders^{3,4} at bathyal depths, a variety of deep-sea communities may be similarly adapted. These findings could affect predictions of the impact of human activities, such as waste disposal or manganese nodule mining, on deep-sea communities.

This work was supported by NSF grant OCE 84-07478. We thank R. Hollis and the *Alvin* group, G. Smith, J. Hampel, R. Hessler and S. Veress for technical assistance, and R. Wheatcroft, P. Hill and D. Penry for reviewing the manuscript. Contribution 1636 from the School of Oceanography, University of Washington.

Received 9 May; accepted 3 June 1986.

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