

Dynamics of surficial trace assemblages in the deep sea

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Abstract—We present a steady-state model addressing factors that determine surficial trace concentration (fraction of sea floor covered by tracks and trails) relative to the areal density and composition of mobile epibenthic megafauna. Trace concentration is posited to be a direct function of the mean production rate of new traces and their mean residence time. Production rate, in turn, is governed by the density of trace makers, their average width and rate of movement, and the fraction of available (i.e. untracked) space on the sea floor. Trace-maker density is not solely a function of epibenthic megafaunal density, but is also influenced by the microscale roughness of the sediment surface; as roughness increases, a higher proportion of mobile epibenthos (although deforming the sediment surface) do not leave recognizable traces. Trace residence time is controlled by the combination of three destructive mechanisms: diffusive sediment mixing by infauna, retracking by epifauna, and physical reworking.

Explicit predictions of the model are supported by new survey and time-series data from two deep-sea sites that differ radically in epifaunal abundance, Santa Catalina Basin (1300 m, east Pacific) and the HEBBLE area (4800 m, west Atlantic). In the former, due to high sediment roughness, a large proportion of the abundant epibenthic megafauna do not produce recognizable traces; thus trace production rate is low and trace destruction is dominated by retracking. This combination results in a low mean trace concentration (1% of sea floor surface area) relative to the density of epibenthic megafauna (16.5 m^{-2}). In the latter region, a much smoother sediment surface results in trace production by most epifaunal taxa. The extremely abundant and active infauna at this site, however, produce high sediment mixing rates and thus low trace residence times and concentrations (5% of sea floor surface area). Application of a steady-state model to data from the HEBBLE region is validated by solving for the unsteady case and showing that approach to equilibrium trace concentration is essentially (95%) complete only 10 days after a benthic storm erases all traces. Previous studies of deep-sea lebensspuren and megafauna prove consistent with the model.

INTRODUCTION

TRACKS and trails produced in surface sediments by deep-sea animals are important for diverse reasons. By enhancing sediment microtopography, animals decrease the critical velocity necessary to erode very fine sands (NOWELL *et al.*, 1981; LUCKENBACH, 1986). Sediment disruption by epi- and infaunal organisms may also be a significant agent in structuring soft-bottom benthic communities (BRENCHLEY, 1981; THAYER, 1983; SMITH *et al.*, 1986). More directly, traces left by epifaunal animals often provide the only evidence of their past existence, especially in the deep sea where chemical dissolution of hard parts and scavenging are prevalent. This fact has led some authors (e.g. YOUNG *et al.*, 1985) to postulate that trace density might serve as a surrogate measure of epibenthic biomass. Such a use implies that the relationship between trace-maker abundance and trace density is well known. The few studies that have measured both variables,

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however, usually reveal a seeming paradox: epibenthic megafaunal abundance and trace density or concentration often are inversely related (KITCHELL *et al.*, 1978; YOUNG *et al.*, 1985). MAUVIEL and SIBUET (1985) did not observe this negative correlation, but neither do their data support a direct relationship.

Basic data concerning rates of trace production and destruction, and trace residence times are lacking. There exists, moreover, no conceptual framework to guide future studies or to identify important but as yet unmeasured parameters. The immediate goal of this paper is to build such a framework. The intent is to allow generalization and prediction regarding the relationship between megafaunal abundance and trace concentration. After constructing the formal model, we test our predictions against new photographic survey and time-series data collected from two functionally different deep-sea areas.

DEVELOPMENT OF THE MODEL

We wish to predict the effects of different faunal abundance and community composition on trace concentration in the deep sea. We restrict our model to megafauna that move on or along the sediment–water interface and the traces they produce. Thus, infauna or permanently sessile epifauna, such as actinians, and biogenic structures that are maintained for some time by animals (e.g. domichnia or agrichnia, EKDALE, 1985) are not treated in this model. As we formulate the model we will make certain assumptions in order to allow analytical solutions from data at hand. The validity of these idealizations and the sensitivity of the model's results to them will be explored in the discussion, though we stress at the outset that availability of additional data in the future will allow many of the assumptions to be relaxed, complicating the model but giving more precise and accurate results. In particular we deal primarily with averages, foregoing the frequent convention that denotes mean quantities with an overbar.

At steady state, average trace concentration (C) at any one time depends upon the mean production rate of new traces (P_{new}) multiplied by their average residence time (T):

$$C = P_{\text{new}} T, \quad (1)$$

where production rate is expressed as area of trace created per unit of area of sea floor per day (T^{-1}), residence time is expressed in days (T), and concentration is area of trace per unit of sea floor area (dimensionless). Because traces are manifested as areas of modified sediment on an essentially planar surface, we quantify their abundance as the proportion of sea floor area covered by traces (i.e. trace concentration) rather than by, say, trace density (i.e. number m^{-2}). Otherwise, problems arise when, for example, a simple plowmark is cut in half, thus decreasing trace concentration but *increasing* the numerical density of traces.

Trace production rate

The rate at which new traces are produced is dependent upon several related factors: the abundances and types of epibenthic megafauna, the average rate that these animals move over the sediment surface, the average width of trace produced, and the fraction of available (i.e. untracked) space on the sea floor. The first two variables are of broad importance and are commonly measured, while the others take on significance only in

the present context. New trace production rate is related to the above parameters in the following manner:

$$P_{\text{new}} = N_p VW(1 - C), \quad (2)$$

where the first term, N_p , represents the mean number of trace producers m^{-2} , V is average crawling rate (m s^{-1}), W is a measure of the mean trace width expressed on a per individual basis (m ind^{-1}), and $1 - C$ is the fraction of untracked space (C ranging from 0 to 1).

Clearly, the density of mobile epibenthic megafauna will affect resultant trace production rates. Of equal importance, however, is the composition of the megafaunal community, because not all animals are equivalent in their trace-producing potential. Surface markings left by some animals are more recognizable than those left by others, based on factors related to animal size, mechanics of locomotion, and microscale sediment roughness. On a perfectly smooth surface, any animal that deforms the surface will leave a recognizable trace (Fig. 1a,b). As the microscale roughness increases, however, some animals will deform the sediment but leave no recognizable trace; the signal will be lost in the noise (Fig. 1d). Thus, a subset of the total mobile, epibenthic megafauna (N_t) may or may not produce recognizable traces, depending on sediment

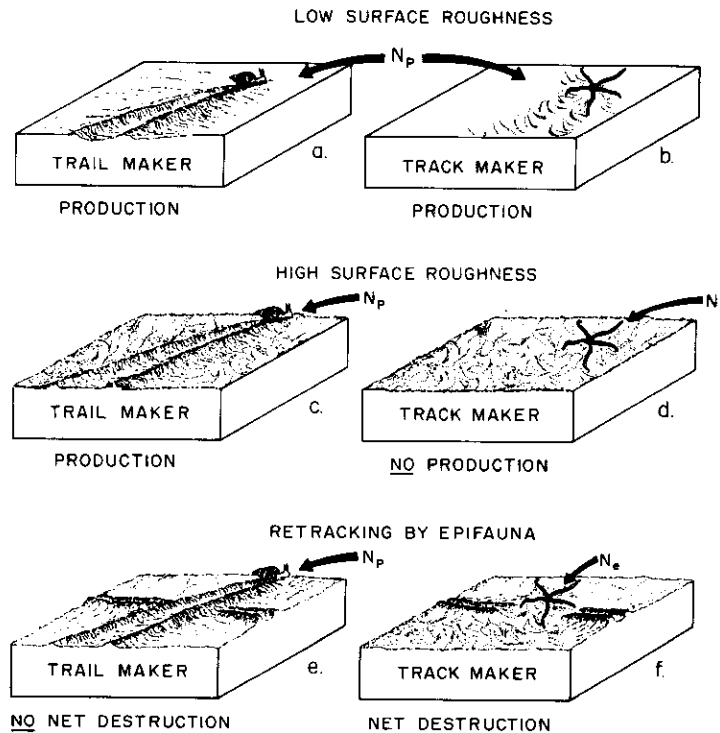


Fig. 1. Schematic cartoons illustrating processes of trace production and destruction. (a,b) At low sediment roughness all mobile epifauna (trail makers and track makers) produce recognizable traces. (c,d) With increasing sediment roughness some taxa (track makers) no longer produce recognizable traces (d). These taxa then fall into the N_e category. (e,f) Net destruction of traces due to retracking by epifauna only occurs due to N_e taxa (f). See text for greater details.

Table 1. Qualitative categorization of common deep-sea taxa according to whether they are obligate or contingent trace producers. Taxa on the left always produce recognizable traces regardless of the sediment microtopography. As sediment roughness increases taxa on the right shift from being trace makers to being N_e taxa

Obligate taxa	Contingent taxa
Gastropods	Crustaceans
Bivalves	Ophiuroids
Echinoids	Holothurians
Enteropneusts	Asteroids

roughness. This subset we term "contingent trace makers" (Table 1). For a given roughness, a fraction of the contingent trace makers will fall into a non-trace-producing category, N_e (where "e" stands for "erasers" as explained below), with the remainder falling in the trace producer pool (N_p) (Fig. 1c,d). As roughness increases, more contingent trace makers will fail to produce recognizable traces, yielding an increase in N_e and a corresponding decrease in N_p . In this notation, the total epibenthic megafauna (N_t) is comprised of trace producers (N_p) and non-trace producers (N_e), with $N_t = N_p + N_e$.

This bipartite subdivision is analogous to one employed in ichnology, where a *trackway* represents a series of discontinuous, low-relief impressions in the sediment, while a *trail* represents a continuous groove in the sediment (FREY, 1973). Animals that produce trackways are contingent trace makers (i.e. they can fall into the N_e or N_p category depending on microtopography), while trail makers always are in the N_p pool. It is the density of non-trace-producing animals (N_e) subtracted from the total density of epibenthic megafauna (N_t) that scales new trace production rate. Equation (2) then can be rewritten as

$$P_{\text{new}} = (N_t - N_e) VW(1 - C). \quad (3)$$

Moreover, because the microscale roughness of the sediment surface is likely a direct function of N_t , N_e/N_t increases with increasing N_t , because more animals fall into the N_e category with increasing sediment roughness.

The last two variables needed to characterize the problem are the average crawling speed (V) and the average trace width per individual (W). Data collected from *in situ* time-series photographs of average epibenthic megafaunal crawling rates are summarized in Table 2. Speeds are highly variable within and between taxa, and even within a single species (ROWE *et al.*, 1974). For this reason confidence intervals around any average value will remain large. Data pertaining to average trace widths also are sparse. Again, the amount of variation in this parameter is likely to be large because of broad ranges in the size of epibenthic megafauna (LAMPITT *et al.*, 1986). We note, however, that because our model is based on mean values of crawling speed and width, high variance in these parameters is not of great concern.

Trace residence time

Trace residence time is the period during which a trace is recognizable (e.g. from photographs) on the sea floor before it is destroyed. Surficial traces can be destroyed in three ways: through tracking over by other epibenthic megafauna; through grain-by-grain

Table 2. Summary of crawling rates of various deep-sea taxa from the literature and this study

Taxon	Speed (cm min ⁻¹)	Depth (m)	Reference
Ophiuroid	6.0	1180	BRUCE (1962)
<i>Ophiomusium lymani</i>	0.7-3.4	1200	LAFOND (1967)
<i>Scotoplanes</i> sp.	0.6	1200	LAFOND (1967)
"Green worm"	2.9	360	ROWE <i>et al.</i> (1974)
<i>Cancer borealis</i>	7.7	360	ROWE <i>et al.</i> (1974)
Hemichordate	0.2	4873	PAUL <i>et al.</i> (1978)
Holothurian	0.1	4906	THORNDIKE <i>et al.</i> (1982)
Shrimp	1.7-4.5	2664	LAMPITT and BURNHAM (1983)
<i>Bathybembix bairdii</i>	1.5	1300	This study (SCB)
<i>Neptunia amianta</i>	1.4	1300	This study (SCB)
Gastropod sp. A	1.0	4800	This study (HEBBLE)
Gastropod sp. A	0.2	4800	This study (HEBBLE)
Megafauna	0.7	4800	This study (HEBBLE)
Gastropod sp. B	0.1	4800	This study (HEBBLE)
Decapod	1.6	4800	This study (HEBBLE)
Ophiuroid	0.4	4800	This study (HEBBLE)

collapse due to diffusive, subsurface mixing; and through physically mediated erosion and deposition.

As animals move over the sediment surface and cross traces, they partially or totally destroy pre-existing tracks and trails. What remains in place of the old trace is dependent upon the identity of the crossing animal (Fig. 1e,f). If, for example, the animal crossing a trace is an N_p taxon, then the area of the old trace crossed by the animal is replaced by a new trace and no net trace production or destruction occurs. (Note that new trace production occurs only outside the area of the old trace, as described by equation 3.) It is taxa in the N_e category (i.e. non-trace producing under the local sediment roughness conditions) that erase traces but leave nothing recognizable in their place (Fig. 1f). Thus, it is the density of these animals (N_e), their average crawling speed (V), their average width (W), and the concentration of traces (C) that control net trace destruction rate (D_{trax}) due to tracking:

$$D_{\text{trax}} = N_e V W C. \quad (4)$$

At steady state, destruction rate must balance production rate; thus an expression for trace residence time, when tracking is the predominant destructive mechanism, can be derived by rearranging equation (1)

$$T = \frac{C}{D_{\text{trax}}} \quad (5)$$

substituting for D_{trax} yields

$$T = \frac{C}{N_e V W C} \quad (6)$$

or

$$T = \frac{1}{N_e V W}. \quad (7)$$

Substituting the trace production (equation 3) and residence time (equation 7) expressions into equation (1) yields

$$C = [(N_t - N_e) V W (1 - C)] \left[\frac{1}{N_e V W} \right]. \quad (8)$$

There is no *a priori* reason to believe that V and W (which are mean quantities) vary significantly between N_p and N_e taxa; if they are assumed to be equal, they drop out of the problem. Again, as more data become available, this simplifying assumption can be relaxed. After rearranging terms,

$$C = 1 - \frac{N_e}{N_t}. \quad (9)$$

Thus, the ratio N_e/N_t , rather than the magnitude of N_t alone (YOUNG *et al.*, 1985), determines trace concentration when destruction due to tracking dominates.

The second trace destruction mechanism, diffusive sediment mixing, does not depend on the density and activity of the epifauna. CULLEN (1973) called attention to the ability of meiofauna to smooth and eventually erase surficial biogenic structures through small-scale, grain-by-grain jostling of particles. This mechanism extends to larger animals, as illustrated by the experiments of CLIFTON and HUNTER (1973). They qualitatively monitored the disappearance rates of artificially formed "ripples" in four subenvironments of a patch reef. Their results are of interest in two respects: disappearance rates between and among sites varied by more than a factor of two, suggesting spatial variability in the intensity of the driving mechanism; and, the area with the fastest bedform disappearance rates had the finest sediment and, by implication, the highest infaunal density (CLIFTON and HUNTER, 1973).

Subsequent to these studies, models of sediment mixing by animals have evolved considerably, and explicit measures of mixing intensity have been derived. Bioturbation is now most often modeled as a one-dimensional (vertical) diffusive process, and mixing intensity is represented by a biodiffusivity value (D_b) analogous to the standard Fickian diffusion coefficient (BOUDREAU, 1986). Thus, as MAUVIEL and SIBUET (1985) have suggested, it is likely that mixing intensity (D_b) and not infaunal density determines trace residence times. Some measure of trace size (e.g. cross-sectional area or volume) also will affect disappearance rates since diffusion rate is length-scale dependent. The exact form of the relationship between mixing intensity (D_b), trace cross-sectional area (A), and trace destruction rate (or residence time) is the subject of a following paper (WHEATCROFT, in preparation) and beyond the scope of this work. For present purposes, let trace destruction rate due to mixing (D_{mix}) follow the relationship

$$D_{mix} = \left[f_1 \left(\frac{D_b}{A} \right) \right] C, \quad (10)$$

where D_b has units of $\text{cm}^2 \text{y}^{-1}$, A is cm^2 , and f_1 is a coefficient of proportionality.

Traces can also be destroyed by physical mechanisms; through sediment accumulation, erosion or physical reworking (erosion plus deposition). Because biologically mediated trace residence times are relatively short (see below), however, and typical deep-sea sediment accumulation rates are very slow ($<20 \text{ cm ky}^{-1}$), it is doubtful that net

deposition could be important in destroying traces. Erosion or reworking of surficial features, however, can be important in very dynamic areas of the deep sea. Such areas would include deep western boundary areas influenced by benthic storms (HOLLISTER and MCCAVE, 1984; NOWELL and HOLLISTER, 1985). The few data pertaining to the regularity of such events suggest that they are not frequent enough in the deep sea to overshadow the biological mechanisms of trace destruction, as our own later analysis of the unsteady case will demonstrate.

End-member examples

When physical mechanisms of trace disappearance are unimportant, the change in trace concentration with time is the difference between the production term (equation 3) and the destruction terms due to tracking (equation 4) and mixing (equation 10). In differential equation form this relation is

$$\frac{dC}{dt} = [(N_t - N_e) V W (1 - C)] - [N_e V W C] - \left[f_1 \left(\frac{D_b}{A} \right) C \right]. \quad (11)$$

If we assume steady state ($dC/dt = 0$) and that V and W do not vary between N_p and N_e taxa, then the production and destruction terms can be set against one another and manipulated algebraically to obtain

$$C = \frac{1 - N_e/N_t}{1 + D_b^*}, \quad (12)$$

where $D_b^* = f_2(D_b/N_t V W A)$, is non-dimensional, ranges from 0 to infinity, and represents the ratio between disappearance rate due to diffusive mixing and production rate of surficial features, f_2 being another coefficient of proportionality. Figure 2 is a

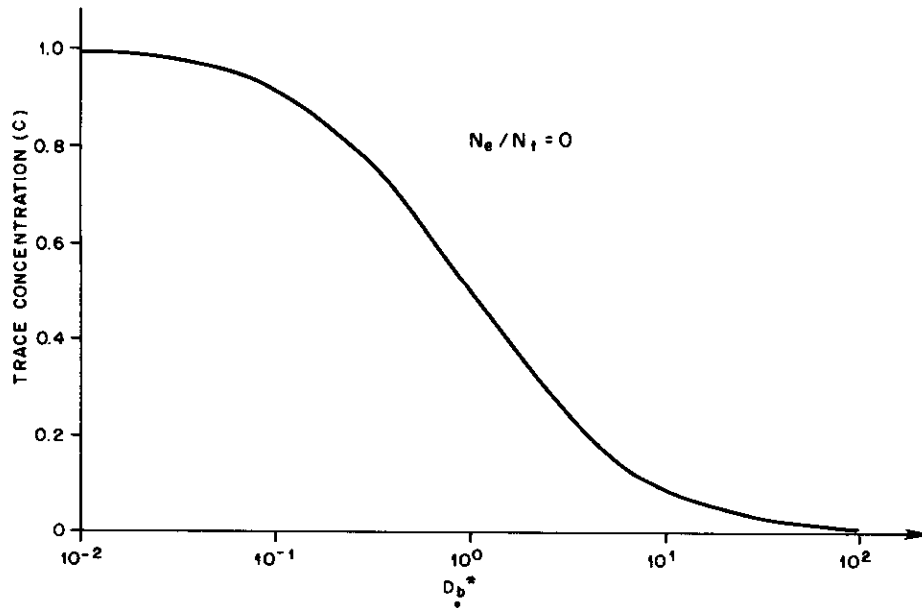


Fig. 2. Semi-log plot of trace concentration as a function of D_b^* for cases in which $N_e/N_t = 0$.

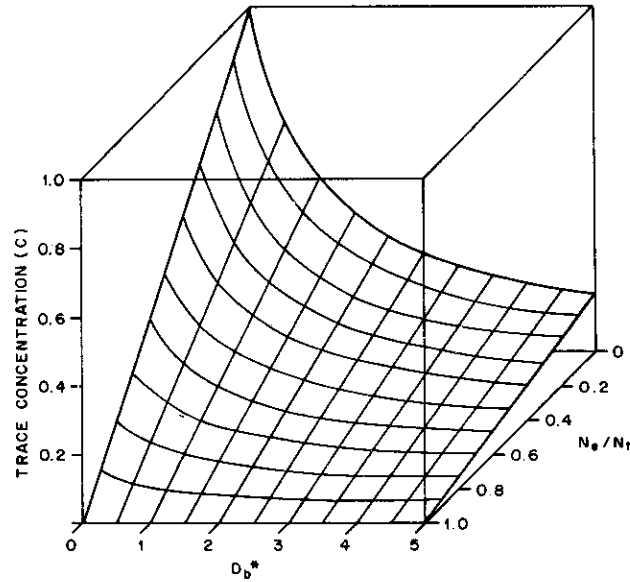


Fig. 3. Trend surface of trace concentration as a function of N_e/N_t and D_b^* . Note that D_b^* ranges to infinity (cf. Fig. 2) but is only depicted up to 5 in this plot.

semi-log plot of D_b^* vs trace concentration (C) when $N_e/N_t = 0$. The term in the numerator of equation (12) was derived earlier (equation 9). It characterizes the system when N_t is large, N_e is non-zero, and tracking dominates disappearance rates (i.e. when D_b^* approaches zero). Figure 3 is a trend surface of trace concentration vs N_e/N_t and D_b^* . It can be used to predict trace concentration when reasonable estimates of values along the other axes can be obtained.

In a case where there are many epibenthic megafauna, most of which are in the N_e category due to high sediment roughness, N_e/N_t approaches unity, and trace concentration is low regardless of the value of D_b^* . In areas where N_e/N_t approaches zero and D_b^* is less than one, trace concentration is quite high. Alternatively, N_e may be zero even at high trace concentrations (i.e. on rough sediment surfaces) if only trail makers comprise the epibenthic community. At low tide, many intertidal mudflats dominated by trail-producing gastropods have very high trace concentrations (FREY *et al.*, 1987) for this reason.

STUDY SITES AND METHODS

Two functionally different deep-sea areas were chosen to test the model explicitly. The first, Santa Catalina Basin (SCB), is one of several bathyal basins in the California continental borderland (Fig. 4a). The floor of the main basin is nearly flat and lies at approximately 1300 m water depth. Sediment in SCB is poorly sorted, clayey silt with a mean disaggregated particle size of 4 μm . Bottom waters are oxygenated (0.4 ml l^{-1} , SMITH *et al.*, 1983), and organic carbon flux to the bottom is high, resulting in an abundant and moderately diverse benthic fauna (JUMARS, 1976; SMITH and HAMILTON, 1983; SMITH, 1986). Studies of sediment mixing rates from a nearby site (D. J. DEMASTER, personal

communication, 1987) show high values relative to other deep-sea settings. Epibenthic megafauna, particularly brittle stars, are especially abundant (SMITH and HAMILTON, 1983; SMITH, 1985).

Vertically oriented, survey-type bottom photographs were obtained from the central portion of the basin (site A, Fig. 4a) on *Alvin* dives 1205 and 1206 (12–13 March 1982). A Benthos model 372 camera was mounted on *Alvin*'s basket, where it took photographs approximately every 8 s as the submersible skied slowly across the bottom. Several hundred square meters of bottom were photographed. At times, however, the submersible drifted slightly (1–2 m) off the bottom, resulting in increased coverage but diminished resolution of the photographs. In order to attain reasonable consistency and allow comparison with photographs from the other study site, images that covered more than 3 m² were disregarded. This criterion reduced the number of usable photographs to approximately 100. Of them, 23 images, representing an area of approximately 44 m², were selected at random for further analysis. Areal coverage of each photograph was

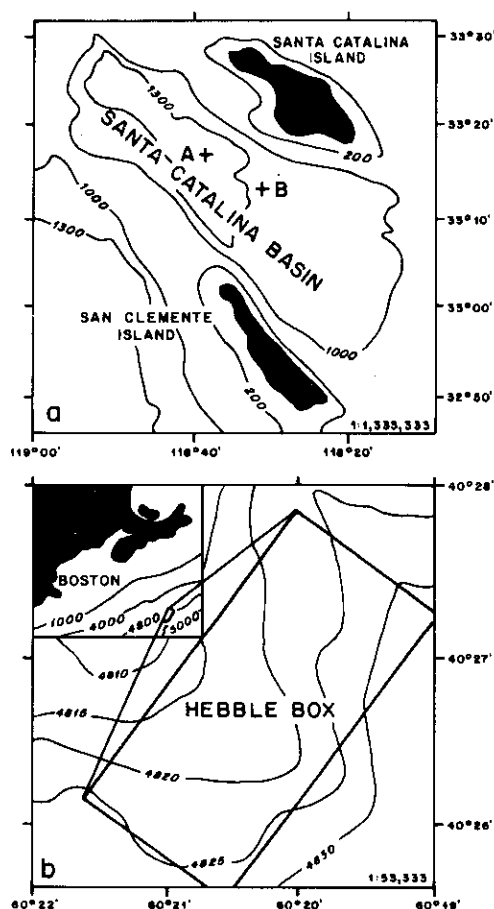


Fig. 4. Bathymetric map of study sites: (a) Santa Catalina Basin (located approximately 100 km SSW of Los Angeles) dive site (A) and the time-series site (B), and (b) the 4 × 2 km HEBBLE BOX. Contours in meters.

estimated by measuring the disk diameters of over 10 *Ophiophthalmus normani* (a brittle star) within each image. They were then compared to an average value of 10.5 mm taken from over 450 individuals (SMITH, 1983) and used to calibrate each photograph. The robustness of this approach is supported by the megafaunal densities reported below, which compare well with those of SMITH and HAMILTON (1983).

Qualitative information concerning trace destruction mechanisms was obtained from a slightly shallower part of SCB (site B, Fig. 4a) in the form of time-lapse photographs of a small area of the sea floor. Because this site differs significantly from site A in terms of total epibenthic megafaunal density and composition (C. R. SMITH, unpublished data), we felt that quantitative inter-site comparisons were unjustified.

The other study area lies at the foot of the Nova Scotian rise at approximately 4800 m depth and is part of the High Energy Benthic Boundary Layer Experiment (HEBBLE) site (Fig. 4b). The HEBBLE area has recently been shown to be an episodically dynamic sedimentary environment, with recorded near-bottom currents in excess of 30 cm s^{-1} (NOWELL and HOLLISTER, 1985). Analyses of the macrofauna, meiofauna and bacteria show conspicuously high abundances relative to other abyssal sites (THISTLE *et al.*, 1985; THISTLE and SHERMAN, 1985; REIDENAUER and THISTLE, 1985). DEMASTER *et al.* (1985) also report anomalously high mixing rates for a deep-sea setting. The megafauna have not been formally studied.

Survey-type bottom photographs were obtained from the principal HEBBLE study region, known as the "HEBBLE box" (HOLLISTER and McCAVE, 1984), during *Knorr* cruise 96 (July 1982). A standard bottom-contact-activated camera system was used to obtain over 300 usable photographs. From them 67, representing 27 m^2 , were selected at random for further analysis. Time-series stereophotographs were taken with two Benthos survey cameras (Model 377) mounted 1 m apart on a free vehicle. These stereophotographs were obtained every hour for a period of 113 days.

In photographs from both areas, traces and animals down to 5 mm in size could be resolved and counted. Areal coverage of traces was measured using a Motion Analysis (VP-310) video processor interfaced with a Sun III work station. For each photograph, grazing, resting and crawling traces were outlined. In addition, areas of the sea floor that were either under- or over-exposed or obscured by the compass or data chamber were also outlined. These shapes were then digitized and fed into a FORTRAN 77 program that calculated areas. Replicate digitizations produced a coefficient of variation less than 5%. The total area of sea floor covered by traces was then divided by the total area of visible bottom to give trace concentration.

Data therefore consist of two types: single-lens, survey-type photographs (that cover a large area of the sea floor and from which trace concentration and megafaunal density were measured) and time-series photographs of a small area of the bottom (from which trace production rates, residence times and destruction mechanisms were estimated).

RESULTS

Santa Catalina Basin

The floor of SCB is characterized by large numbers of mobile epibenthic megafauna (Fig. 5a). The activities of these animals and the abundant infauna result in an extremely rough sediment surface, a microtopography that is clearly biologically controlled. Furthermore, SCB is a physically quiescent area in which near-bottom currents have not

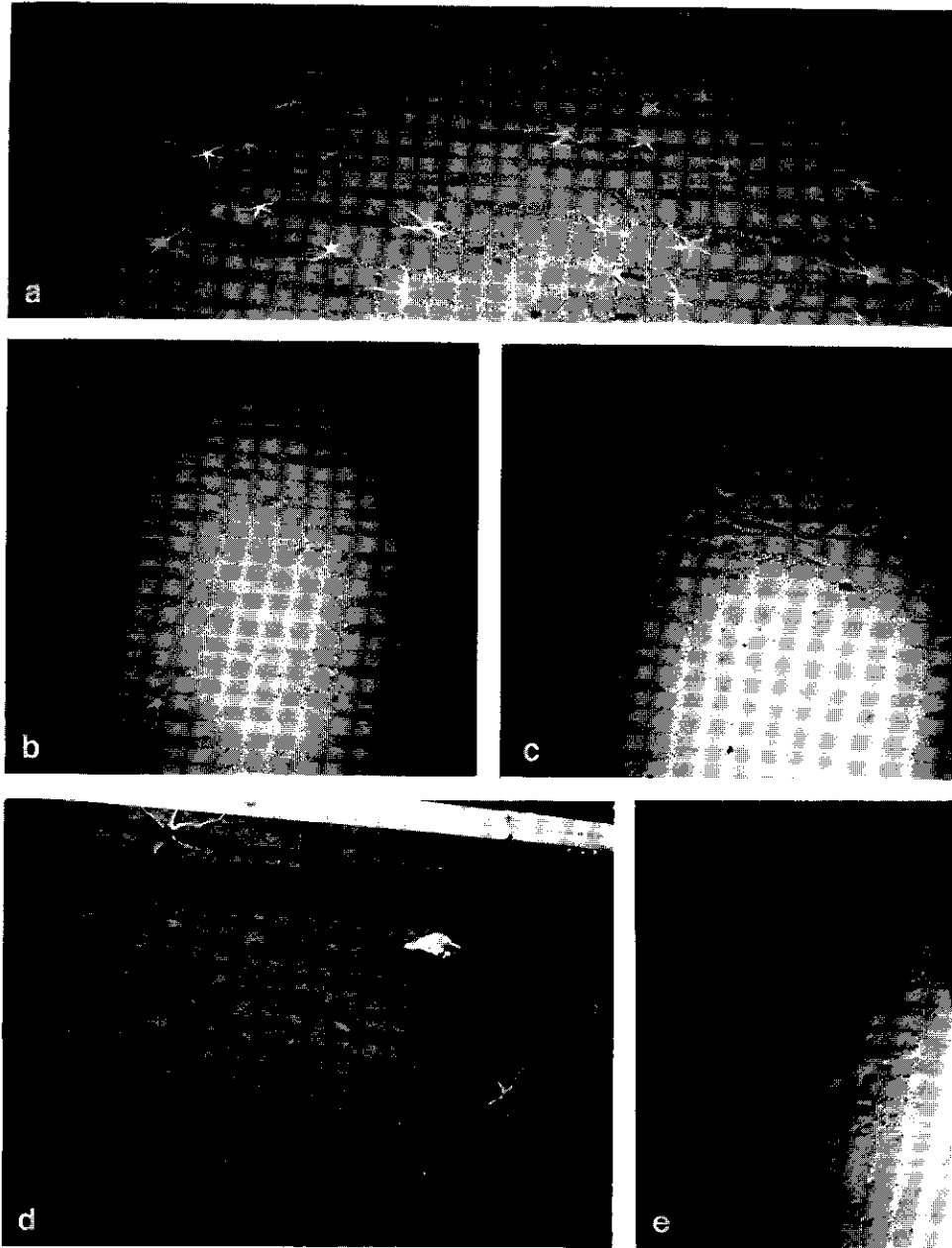
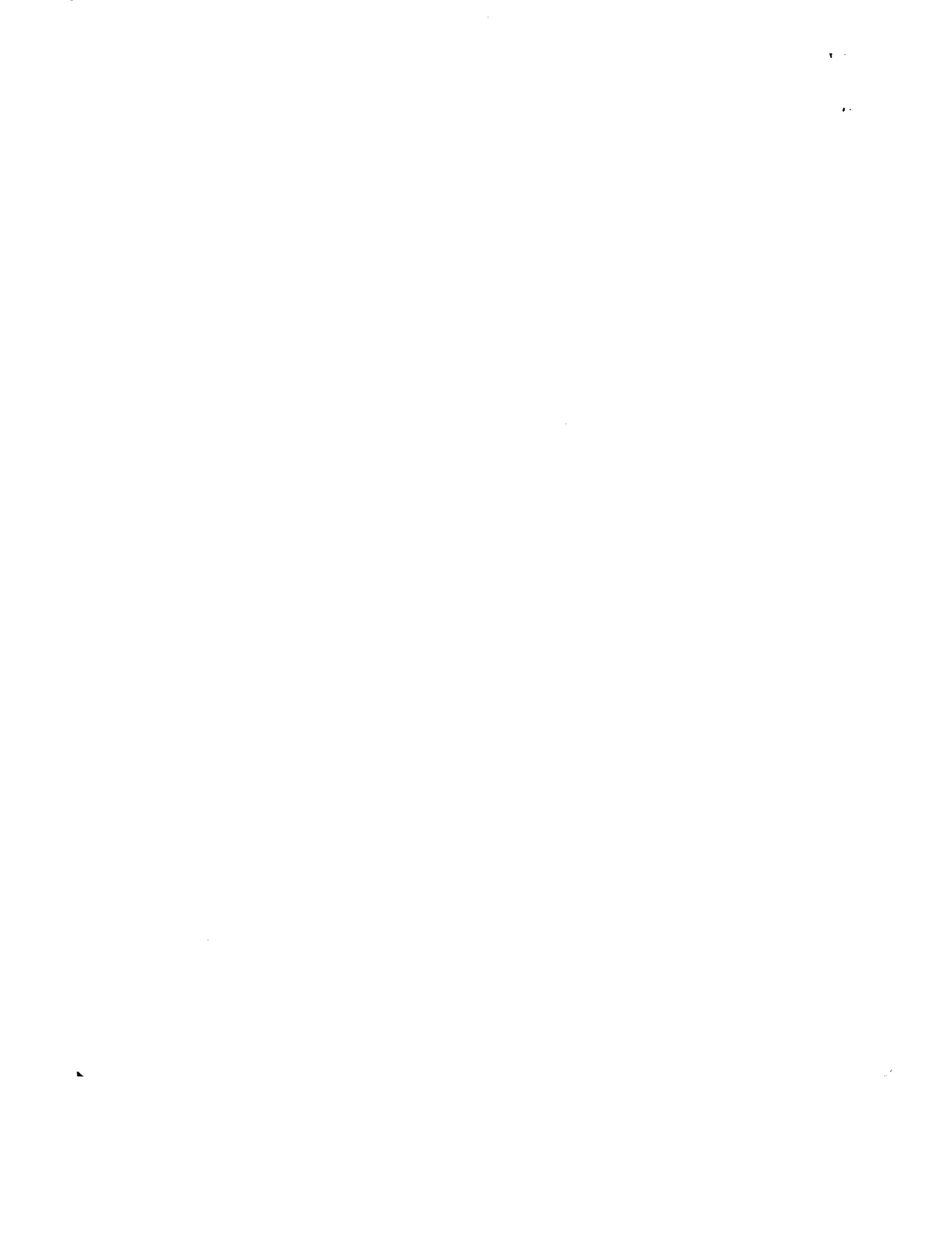


Fig. 5. Characteristic traces and megafauna. (a) Oblique view of the SCB sea floor showing *Scotoplanes globosa* (lower left), *Pandalopsis ampla*, numerous *Ophiophthalmus normani*, and abundant maldanid tubes. Note the high roughness of the sediment surface. (b) Vertical photograph from the HEBBLE area, showing an unidentified ophiuroid leaving a series of resting marks and the trackway of a probable brachyuran crab (upper right). (c) Vertical photograph from the HEBBLE area showing a "mole trail", an ophiuroid resting mark, and furrows (upper right). (d) Vertical photograph of SCB sea floor with *Neptunia amianta* and its trail and several *O. normani*. (e) "Feather-stitch" trail from the HEBBLE area.



been observed to exceed 10 cm s^{-1} (personal observation during more than 30 *Alvin* dives). Overall (areal mean) sediment roughness is relatively constant in time, although it may change considerably on spatial scales less than 10 cm. This temporal stability allows categorization of epibenthos as N_e or N_p taxa with reasonable certainty.

The community is dominated by *Ophiophthalmus normani*, which occurs at a mean density of 16.4 m^{-2} and makes up nearly 99% of the epibenthic megafauna. Due to the high sediment roughness, this brittle star, like others in the basin, does not leave recognizable traces. In moving about the sediment surface, however, it destroys pre-existing tracks and trails and thus falls into the N_e category. Other mobile epibenthic megafauna in the basin (SMITH and HAMILTON, 1983 and submersible-based personal observation) include several other species of ophiuroids, the large gastropods *Neptunia amianta* (Fig. 5d) and *Bathybembix bairdii*, the elasipod holothurians *Scotoplanes globosa* and *Pannychia* sp., a chiridotid holothurian, *Chiridota* cf. *pacifica*, the shrimp *Pandalopsis ampla*, and several species of asteroids and benthopelagic fishes. Our estimate of total epibenthic megafaunal density (N_t) is 16.5 m^{-2} , a figure close to that obtained by SMITH and HAMILTON (16.7 m^{-2} , 1983) from the same part of the basin.

Despite the large number of mobile epibenthos, recognizable traces are produced by only the two gastropods, *Neptunia* and *Bathybembix*, and the chiridotid. All other taxa of potential trace makers fall into the N_e category due to high sediment roughness. Gastropod traces are most common and easily recognized, consisting of two lateral ridges (about 1 cm in height) separated by a broad (1–2 cm wide) valley (Fig. 5d). The chiridotid trail is slightly less common and is produced by the animal moving just under the sediment surface, although it frequently is in sight. It produces a meandering trail consisting of irregularly spaced, sometimes paired, ovoid lobes of sediment, similar to the ichnogenus *Neonereites* reported from many deep-water facies throughout the Phanerozoic (cf. BENTON, 1982, Fig. 5d, e).

In the context of the present model, the epibenthic megafaunal community in SCB has a high total density ($N_t = 16.5 \text{ m}^{-2}$) and a high N_e/N_t ratio (0.99). The time-lapse photographs from site B indicate that this community is one in which destruction of traces is dominated by retracking. Therefore D_0^* , the dimensionless number expressing the ratio of mixing rate to trace production rate, can be scaled out of the problem, allowing a unique solution of equation (11). Predicted trace concentrations are approximately 0.01. This figure is very close to the measured mean trace concentration of 0.0097 (S.D. = 0.019) obtained from the survey photographs.

HEBBLE

The ocean floor in the HEBBLE area differs considerably in almost all respects from that of SCB. The photographic survey shows that mobile epibenthic megafauna are relatively sparse, in sharp contrast to the conspicuously high micro-, meio- and macro-infaunal abundances reported from the HEBBLE area (THISTLE *et al.*, 1985; THISTLE and SHERMAN, 1985; REIDENAUER and THISTLE, 1985). The density of epibenthic megafauna is approximately 0.5 m^{-2} , a figure comparable to many other abyssal sites (cf. ROWE, 1983), but some three orders of magnitude below that observed in SCB. Mobile epibenthos actually photographed (as opposed to inferred as present from characteristic traces) include an ophiuroid, a gastropod and several unidentified animals. In addition, a small (<2 cm long) benthopelagic, shrimp-like animal was observed in many photographs hovering slightly off the sediment surface. With the exception of this animal

(comprising N_e), all mobile epibenthos observed in the survey photographs produced recognizable traces.

The most abundant trace is a simple, relatively straight, bilobed form (group III-B13 of EWING and DAVIS, 1967) of unknown origin. The next most abundant trace, consisting of two ridges separated by a flat-floored medial valley, is probably produced by gastropods. Other traces include ophiuroid tracks and resting marks (Fig. 5b,c), brachyuran crab trackways (Fig. 5b), a mole-like trail of unknown origin similar to the chiridotid trail from SCB (Fig. 5c) and a "feather-stitch" trace (Fig. 5e) referable to EWING and DAVIS's (1967) group III-A7.

Because the HEBBLE area is an episodically dynamic environment (HOLLISTER and McCAVE, 1984; NOWELL and HOLLISTER, 1985), we felt there might be some problem in using a steady-state model, and our time-series data qualitatively showed some temporal variation in bottom roughness. During days 89–96 of the time-lapse deployment, suspended sediment concentrations were so high that the bottom was not visible from 1 m away. Immediately following this storm the sediment surface was smooth due to sediment deposition. Microtopographic variability increased rapidly, however, apparently due to the escape responses (from burial) of cumaceans and other macroinfauna. Since sediment roughness increased beyond pre-storm levels, it is likely that contingent taxa shifted into the non-trace-producing pool (N_e). This switch was in fact demonstrated on day 99 when an ophiuroid moved across the field of view without leaving a recognizable track. Earlier in the time series ophiuroids left recognizable trackways and resting impressions, indicating the change in bottom roughness was great enough to influence trace production rate. Some 13 days after the storm, by day 109, recognizable traces were again produced by a decapod (a contingent trace maker). We took this observation to indicate that the sediment roughness had reached a pre-storm equilibrium. Thus, only about 11% of our time-series data were characterized by unsteady conditions, and they were excluded from the analysis.

The time-series data themselves supported our assumption of quasi-steady conditions. By computing trace concentration on a daily basis (Fig. 6) and using the nonparametric

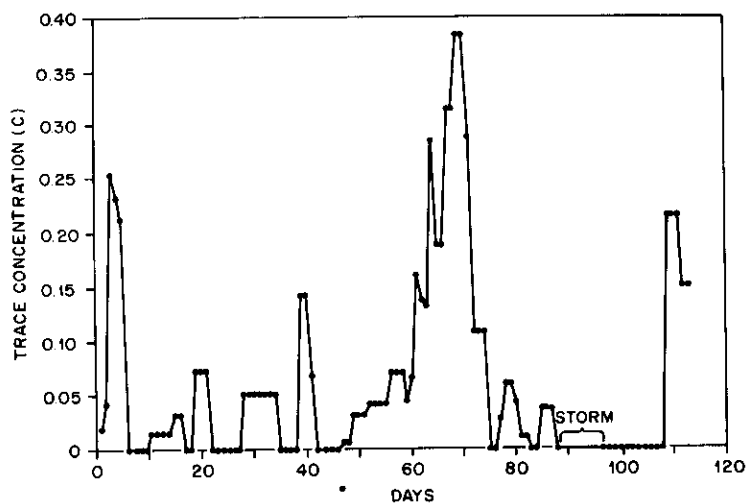


Fig. 6. Record of trace concentration from the HEBBLE site over a 113-day period.

up-down runs test (SOKAL and ROHLF, 1981) we tested for non-randomness of trace concentration over time. Our results show that the observed number of runs (24) falls well within the 95% confidence limits for the expected number of runs (26), giving no reason to suspect a trend or cycle in trace concentration during the time of our deployment.

Explicit testing of the theoretical model as formulated in equations (11) and (12) is not possible, however, because time-lapse photographs showed that traces were destroyed due to diffusive mixing (and not to retracking as in SCB). D_0^* therefore cannot be scaled out of the problem, precluding a unique solution to equation (11). It is possible, however, to test the overall validity of our model (equation 1) by comparing trace concentrations measured from the survey photographs with the time-series data.

From the cumulative frequency distribution of 68 photographs (Fig. 7), mean and median trace concentrations are 0.048 and 0.034, respectively, while graphical 95% confidence limits range from 0 to 0.145. Time-series photographs from the HEBBLE area showed that during the 92 days of approximately steady-state conditions a total of 25 recognizable traces was produced in an area of 0.4 m^2 , yielding an average trace production rate of 0.016 d^{-1} over that period. Trace residence time ranged from 2 to 16 days with an average of 5.1 days (Fig. 8). When these values for mean trace production rate and residence time are put into equation (1), a trace concentration of 0.082 is obtained. This figure falls well into the 95% confidence limits depicted in Fig. 7.

DISCUSSION

Because all models are abstractions of the real world, they are necessarily wrong in some details (Box, 1976). It is thus important to discuss their departures from reality and to evaluate whether these departures are fatal for the purpose at hand. In formulating

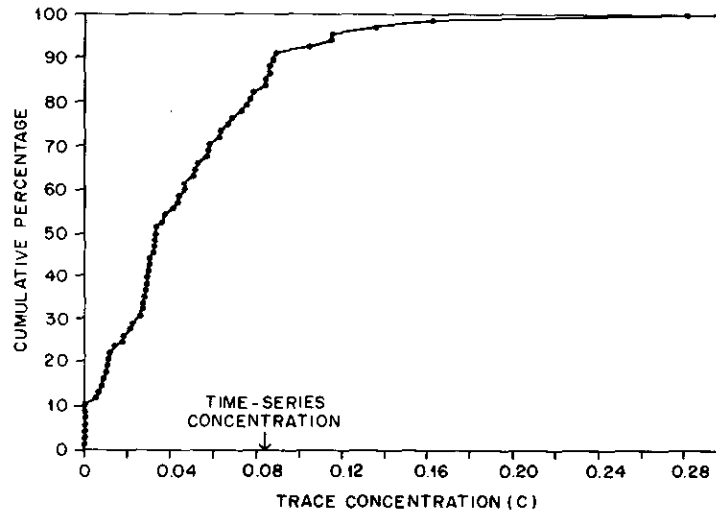


Fig. 7. Cumulative frequency distribution of trace concentrations from photographs within the HEBBLE box and computed trace concentration from the time series data (0.082). Graphical 95% confidence limits from the former range from 0 to 0.145.

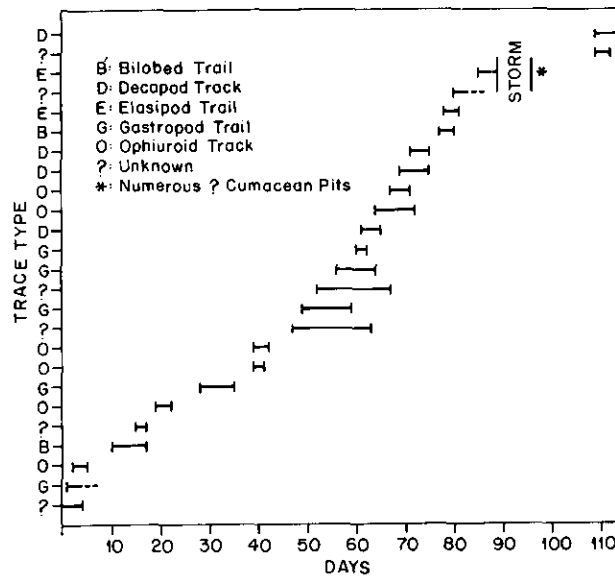


Fig. 8. Running log of the HEBBLE time-series photographs showing time of trace creation, approximate residence time, and probable creator. Bars ending with dashed lines indicate probable erasure by *Sargassum* moving across the bottom

our model we made several simplifying assumptions: (1) N_e and N_p taxa were assigned equal average movement rates (V) and equal mean per individual widths (W); (2) retracking by animals was considered to be 100% efficient as a destructive mechanism, with N_e taxa leaving no replacement traces; (3) sediment microtopography was uniquely related to the magnitude of N_t ; and (4) relevant parameters were at steady state in the deep sea.

By assuming no significant variation between the mean crawling rates and widths of N_e and N_p taxa, we were able to obtain a solution to equation (11). We have done so because there is no *a priori* reason to suspect otherwise. If, however, crawling speed were correlated with body size (V and W covary nonrandomly), then using mean values for these parameters could introduce bias in our predictions. Moreover, if N_e taxa were always significantly larger or move at higher rates than N_p taxa, or vice versa, then our results could once again be in error. Again, it is not difficult to relax this assumption when the existence of data allows it.

Our second assumption, that destruction due to tracking by N_e taxa has a 100% efficiency (is effective in a single pass), also could yield significant bias, especially if animals in the N_e pool were small, slow and inefficient erasers. The match between predicted and observed trace concentrations in SCB does not preclude the violation of this or our first assumption: if animals in the eraser pool (N_e) were faster or larger (on average) than N_p taxa, but erasing efficiency were less than 100%, these biases could counter each other. To redress this potential problem, it would be quite simple to include an efficiency coefficient in equation (4), once data on erasing efficiency became available.

The assumption that certain animals shift into the N_e category as microtopographic variation increases is central to our model. Earlier we had assumed that sediment

roughness was a direct function of epibenthic megafaunal density (N_t), but other factors may contribute to the overall roughness of the sediment surface and thus affect the magnitude of N_e/N_t . Activity by near-surface, infaunal macrobenthos certainly contributes significantly to sediment microtopography (Fig. 5a,d). *In situ* respirometry studies, however, suggest that the densities and activities of infaunal macrobenthos covary positively in space and time with those of epifaunal megabenthos (SMITH and HINGA, 1983). Thus, the trends discussed earlier, where increases in N_t result in increases in N_e/N_t , are likely to be reinforced. Variation in particle size could also affect sediment roughness and trace recognizability, because larger-grained deposits less faithfully record traces (KNOX and MILLER, 1985). Because coarse sediments are almost certainly associated with elevated shear stresses, however, trace destruction rates in such areas may be controlled by physical processes, and our model would not apply.

Finally, we have assumed steady-state conditions to obtain solutions to our model. We do so despite recent evidence that energy level, nutrient flux and community activity (HOLLISTER and McCAVE, 1984; LAMPITT, 1985; SMITH and HINGA, 1983; respectively) in the deep sea can vary temporally. At the SCB study site, however, we are confident (based on numerous *Alvin* dives during various times of the year over a 9-year period) that temporal variations are of second order. On the other hand our time-series data from the HEBBLE site, in conjunction with other studies (HOLLISTER and McCAVE, 1984; NOWELL and HOLLISTER, 1985; GROSS *et al.*, 1988), indicate that microtopography may vary rapidly. If, however, the relaxation time (time necessary to reach equilibrium following a perturbation) is small compared to the period between benthic storms, then an assumption of steady state is indeed reasonable.

We can solve the time-dependent case for HEBBLE by first assuming $N_e = 0$, yielding, from equation (11)

$$\frac{dC}{dt} = [N_t V W(1 - C)] - \left[f_1 \left(\frac{D_b}{A} \right) \right] C. \quad (13)$$

If $K_1 = N_t V W$ and $K_2 = f_1 (D_b/A)$ equation (13) can be rearranged into standard form

$$\frac{dC}{dt} + (K_1 + K_2) C = K_1. \quad (14)$$

This equation then can be solved using an integrating factor (NAGLE and SAFE, 1986) to yield

$$C = \frac{K_1}{K_1 + K_2} + \frac{K_1 B}{e^{(K_1 + K_2)t}}, \quad (15)$$

where B is a constant of integration. Using the initial values that $C = 0$ at $t = 0$ and $C = 0.048$ at $t = \infty$, the amount of time necessary to reach 95% of the equilibrium trace concentration of 0.048 (measured from the survey photographs) is computed to be approximately 8.5 days. Because the period between benthic storms is much longer, of order 100 days (HOLLISTER and McCAVE, 1984), for our model the system can be considered to be generally at steady state. (Note, however, that this simple exercise does not take into account an overshoot in roughness after a storm due to animal escape responses noted previously or the possibility of storm-induced changes in V or D_b .)

Overall, the agreement between our predictions and the observations in SCB and at the HEBBLE site suggests that our assumptions are reasonable or that the model is robust. Our study sites, however, were chosen as end members. SCB is unusual in its very high epibenthic megafaunal density (N_t) relative to other bathyal sites (SMITH and HAMILTON, 1983; SMITH, 1985). This high value of N_t , in concert with abundant (SMITH, 1986) and active (SMITH *et al.*, 1986; D. J. DEMASTER, personal communication, 1987) infauna, results in an extremely rough sediment surface (Fig. 5a,d). Moreover, the community is overwhelmingly dominated by an N_e taxon (*Ophiophthalmus normani*). Thus, N_e/N_t approaches unity, and the trace destruction function is dominated by tracking ($D_{\text{trax}} \gg D_{\text{mix}}$). Conversely, the low epibenthic megafaunal abundance at HEBBLE and consequent low tracking rate allow the abundant (THISTLE *et al.*, 1985) and active (DEMASTER *et al.*, 1985) macro- and meio-infauna to dominate trace destruction through diffusive mixing ($D_{\text{mix}} \gg D_{\text{trax}}$). Thus, the sediment surface at the HEBBLE site remains relatively smooth, allowing most megafauna to leave recognizable traces (N_e/N_t approaches zero).

The majority of deep-sea areas are more likely to lie somewhere in the middle with regard to the prevailing trace destruction mechanism ($D_{\text{trax}} \approx D_{\text{mix}}$). Does our model accurately predict trace concentrations in such cases? Because of the prior lack of a conceptual framework and time-series data, there are no studies in which all of the relevant parameters have been measured. There are several studies, however, in which observations of certain components have been made.

In a comparative investigation of abyssal traces and megafauna from the Arctic Canada Basin and Antarctic Bellinghousen Basin, KITCHELL *et al.* (1978) found that trace "frequency" [defined as high (70–100%), moderate (35–70%) and low (0.35%) areal coverage of the sediment surface] was inversely proportional to organism density (Table 3). At their Antarctic study site (KITCHELL *et al.*, 1978, Fig. 2), we calculate that $N_e/N_t = 0.6$, assuming ophiuroids, decapods and 50% of the holothuroids fall in the N_e category and echinoids, asteroids, gastropods and the remainder of the holothuroids are obligate trace producers. Because we lack any knowledge of the mixing regime at this site, D_e^* could range from 0 to infinity. From Fig. 3, this lack of information would allow trace concentration to range from 0 to 0.4, approximately equivalent to KITCHELL *et al.*'s (1978) reported low trace "frequency". On the other hand, the extremely low densities of megafauna (Table 3) reported from the Arctic Basin suggest that trace destruction there is dominated by mixing. N_e/N_t also might be low; thus nearly all animals would produce traces, along the lines of HEBBLE. Sediment mixing rates would probably (due to presumed lower carbon flux) be lower than at the HEBBLE site, however; thus trace residence times would probably be quite long, and the high trace concentrations observed are to be expected.

Similar comparisons are not possible with YOUNG *et al.*'s (1985) study of the Venezuela Basin, because their data are presented as numbers of traces m^{-2} (observed in photographs) and numbers of megafauna h^{-1} collected by trawling (Table 3). Considering the biases associated with trawl data (RICE *et al.*, 1982), it is impossible to convert these data to meaningful animal densities, and it is not possible to calculate trace concentrations from density information. It is likely, however, that trends in trace concentration qualitatively mimic those in trace density. Thus, the inverse relationship YOUNG *et al.* (1985) observed between megafaunal abundance and trace density is as expected.

Table 3. A summary of photographic studies reporting trace density or concentration and epibenthic megafaunal density from the same site

Reference	Megafaunal density	Trace density or concentration	Study site
KITCHELL <i>et al.</i> (1978)	0.002 m ⁻²	"Moderate" to "high"	Canadian Basin (3700–3840 m)
	0.120 m ⁻²	0.35–1.0 "Low"	Bellinghausen Basin (4000–5000 m)
MAUVIEL and SIBUET (1985)	1.4 m ⁻²	0–0.35 0.6 m ⁻²	Gulf of Gascogne (2100 m)
	0.4 m ⁻²	0.1 m ⁻²	Gulf of Gascogne (2800 m)
	0.7 m ⁻²	0.1 m ⁻²	Gulf of Gascogne (4000 m)
	0.8 m ⁻²	0.4 m ⁻²	Gulf of Gascogne (4700 m)
	0.2 m ⁻²	0.4 m ⁻²	Gulf of Gascogne (4400 m)
	0.3 m ⁻²	0.2 m ⁻²	Gulf of Gascogne (1900 m)
YOUNG <i>et al.</i> (1985)	35.2 h ⁻¹	4.2 m ⁻²	Venezuela Basin (5050 m)
	55.4 h ⁻¹	3.2 m ⁻²	Venezuela Basin (3450 m)
	68.4 h ⁻¹	2.2 m ⁻²	Venezuela Basin (3950 m)
This study	16.5 m ⁻²	0.0097	Santa Catalina Basin (1300 m)
	0.5 m ⁻²	0.048	HEBBLE box (4800 m)

Qualitative support for our model is furnished by EDWARDS (1985). He studied biogenic structures observed in bottom photographs and x-radiographs from Santa Cruz Basin, a dysaerobic basin adjacent to Santa Catalina Basin. Despite the large number of ophiuroids, asteroids and holothurians observed on the basin floor, discrete traces of these animals were difficult to resolve on the sediment surface. In contrast, irregular echinoids and gastropods, although less abundant, left readily apparent trails (EDWARDS, 1985). Thus, it appears that the former groups would be categorized as N_e taxa, while the gastropods and irregular echinoids are N_p taxa.

Processes leading to the destruction of surface traces still on the sediment surface are only the initial "filter" these biogenic structures must pass through if they are to be buried and eventually preserved (EKDALE and BERGER, 1978). Our study serves to identify explicitly trace destruction mechanisms and to put initial estimates on their relative importances. Regardless of which mechanism dominates, it appears that traces not actively maintained by animals are ephemeral features with lifespans measured in days to weeks (not months and years as previously thought; MAUVIEL and SIBUET, 1985). The shortness of trace residence times coupled with intense near-surface mixing (CULLEN, 1973; DEMASTER *et al.*, 1985) suggest little chance of preserving surface traces in the historical record without some event that abruptly eliminates normal mechanisms of trace destruction.

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