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Mobile megafaunal activity monitored with a time-lapse camera in the abyssal North Pacific

K. L. SMITH JR,* R. S. KAUFMANN* and W. W. WAKEFIELD†‡

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Abstract—Epibenthic megafauna comprise a large fraction of the deep-sea benthic biomass and are considered important in bioturbation and sediment mineralization processes. However, the sparse and often patchy distribution of these animals makes them difficult to study on meaningful spatial and temporal scales. We used a new time-lapse camera system to measure the movements of mobile megafauna over a 3-month period across a 20 m^2 area of the abyssal sea floor in the eastern North Pacific. This free-vehicle camera system consisted of a time-lapse camera mounted in a tripod frame with a field marker, time releases and flotation assembly. Time-lapse photographs of the sea floor were taken hourly from March to June 1991 at a station off the central California coast (34°50′N, 123°00′W) at a depth of 4100 m. Megafaunal density reached a peak in April, immediately preceding increased fluxes of particulate organic carbon (POC) and chlorophyll *a* measured in sediment traps at 50 m above bottom. Mobile megafauna were numerically dominated by the holothuroids, *Abyssocucumis abyssorum*, *Peniagone vitrea* and *Elpidia minutissima*. The total area traversed by the megafauna each day was estimated by summing the distance traveled between hourly photographs multiplied by the body width of each animal. Area traversed by the megafauna reached a peak in early May following the peak in faunal density and preceding the peak in POC flux in mid-May. The mobile megafauna traversed 88% of the 20 m^2 area of the sea floor over the 3-month period. Estimates of oxygen consumption for the dominant mobile megafauna revealed that these animals would consume only 1.6% of the particulate organic carbon flux entering the benthic boundary layer. However, the extensive area traversed by the mobile megafauna in a 3-month interval suggests that these animals are important as modifiers of the surface sediment, either through mixing or repackaging of material.

INTRODUCTION

EPIBENTHIC megafauna are conspicuous organisms that occupy the sediment–water interface and can be defined as those animals large enough to be recognized in photographs (typically ≥ 1 cm; GRASSLE *et al.*, 1975; REX, 1981). This group of animals has been shown to comprise a large fraction of the deep-sea benthic biomass in areas of the North Atlantic (HAEDRICH and ROWE, 1977; SIBUET and LAWRENCE, 1981; SIBUET *et al.*, 1984; LAMPITT *et al.*, 1986; RUTGERS VAN DER LOEFF and LAVALEYE, 1986; BILLETT, 1991), Caribbean Sea (RICHARDSON *et al.*, 1985) and in the western Pacific (OHTA, 1983).

Many species of mobile megafauna produce traces across the sediment surface; the density of these traces has been related to faunal abundance (e.g. KITCHELL *et al.*, 1978;

*Marine Biology Research Division, 0202 Scripps Institution of Oceanography, La Jolla, CA 92093-0202, U.S.A.

†School of Fisheries and Ocean Sciences, University of Alaska, Fairbanks, AL 99775-1090, U.S.A.

‡Present address: Institute of Marine and Coastal Science, Rutgers University, New Brunswick, NJ 08903, U.S.A.

YOUNG *et al.*, 1985) and trophic conditions (MAUVIEL and SIBUET, 1985). WHEATCROFT *et al.* (1989) developed a model for describing the dynamics of traces produced by megafauna and concluded that, in addition to the density of trace makers, sediment roughness, diffusive mixing by infauna, retracking and physical reworking affected the trace concentration. Movements of the mobile megafauna can be important in mixing surface sediments both vertically (e.g. MAUVIEL and SIBUET, 1985; SMITH *et al.*, 1986) and horizontally (WHEATCROFT *et al.*, 1990). However, horizontal bioturbation by megafauna is believed to be more important than vertical mixing in early diagenesis at the sediment surface (WHEATCROFT, 1991).

The role of megafauna in the utilization of organic matter has been estimated from oxygen consumption or carbon assimilation rates. Megafauna can be important consumers of organic carbon at abyssal depths in the eastern North Atlantic (KHRIPOUNOFF, 1984) and the central North Pacific (SMITH, 1992), but appear to be less important at bathyal depths in the eastern North Pacific (SMITH *et al.*, 1987).

The contribution of mobile megafauna to benthic processes in the deep sea has been inferred largely from measurements made over narrow spatial and temporal windows or from static observations of traces photographed on the sea floor. To address the question of the functional importance of mobile epibenthic megafauna, we measured the movements of animals across a 20 m^2 area of the abyssal sea floor over a 3-month period in the eastern North Pacific with a new time-lapse camera system described below.

INSTRUMENTATION

Time-lapse cameras have been used over the past four decades to monitor processes on or above the sea floor from shelf to abyssal depths in many areas of the world ocean (e.g. THORNDIKE, 1959; HUNKINS *et al.*, 1960; SESSIONS *et al.*, 1968; ISAACS, 1969). From these initial developments, time-lapse cameras as components of free-vehicle instruments have been used either independently or in conjunction with other sensors to make physical, geological and biological measurements in close proximity to the sea floor over time periods from hours to more than 1 year (Table 1). Most of these studies, over the past 20 years, have used still cameras mounted at oblique angles to photograph areas not disturbed by the free vehicle and to enlarge the field of view. Video cameras also have been used where continuous monitoring of processes was desirable.

Our studies required monitoring the movements of epibenthic megafauna over a large area of the sea floor with fine-scale resolution. A still camera system to meet these criteria required the ability to: (1) take time-lapse photographs of the sea floor at 1-h intervals over a continuous period of 4 months; (2) photograph a large area of the sea floor (*ca* 20 m^2); and (3) resolve objects $\geq$ 1 cm in any dimension within the illuminated field of view on the sea floor. The most critical requirements, which differed from previous studies, were the large field of view combined with the fine-scale resolution. Other studies have reported photographic areas <5 m^2 (Table 1), with the exception of PRIEDE *et al.* (1990), who used a video camera system with a photographic area of 8.9 m^2 to monitor large benthopelagic fish at bait. The camera system we developed to meet the above criteria is described below.

Description of time-lapse camera

Our free-vehicle time-lapse camera system consists of a camera tripod, field marker, precision time releases and flotation array. The structural frame of the camera tripod, 2.8

m high and 2.0 m on a side, is constructed of stainless steel angle (Fig. 1). A time-lapse camera (Benthos Model 377 with 28 mm lens) is mounted obliquely in the apex of the frame and inclined 31° from horizontal with the lens positioned 2 m above the sea floor. The angle of view with this camera and lens is 35° in the vertical and 50° in the horizontal plane. Illumination is provided by two 400-W-s strobes (Deep-Sea Power & Light) mounted on extensions to either side of the camera. The strobes provide a well-illuminated field of view of *ca* 20 m^2, beginning 1.77 m from the front of the camera frame. A timing circuit to synchronize the film advance in the camera and firing of the strobes was built and incorporated into the camera housing, which is powered through an externally-mounted battery pack. Four pressure-compensated rechargeable batteries (Deep-Sea Power & Light) power the strobes and are secured on the lower platform of the tripod.

For a size reference in the field of view, we have developed a retractable fiberglass pole (2.3 m long) with two polyvinylchloride (PVC) rings (21.6 cm dia.) mounted along its length (Fig. 1). This field marker is hinged to the front of the tripod frame and falls to the sediment surface in the field of view after the free vehicle reaches the bottom. After sizing of local "permanent" benthic features over a 3-day period, the marker is then retracted to a vertical position. Removal of the field marker from the field of view is important to minimize its impact on benthic processes.

Ballast for the camera system is suspended between tandem precision time releases centrally located in the tripod frame. The ballast consists of scrap metal contained in a steel canister that hangs *ca* 20 cm above the sediment surface and is isolated from the peripherally-mounted batteries and structural frame of the tripod by a cylindrical polyethylene shield.

The total weight of the camera tripod in water is 236 kg (391 kg in air). The positive buoyancy necessary to overcome this weight and generate sufficient lift is 330 kg, provided by 13 evacuated glass spheres (Benthos 43.2 cm dia.) connected in series on a mooring line 30 m above the tripod. A mast assembly with a submersible transmitter, strobe, flag and glass sphere are connected to the top of the array line for location of the instrument once on the surface.

METHODS

The free-vehicle camera system was deployed for 122 days from 22 February 1991 to 22 June 1991 at an abyssal station in the eastern North Pacific (Sta. M). This station is located off the central California coast at 4100 m depth where there are strong pulses of particulate organic carbon entering the benthic boundary layer in the spring and summer (Smith *et al.*, 1992). The sea floor is a low-energy environment with a mean current speed of 2.7 cm s^{-1} (range of 0–8.2 cm s^{-1}, 2 m above the sea floor) and a silty-clay sediment covering extensive areas of low relief.

The free-vehicle camera system was set to take a photograph of the sea floor hourly over this period and was loaded with color negative film (Fuji, Type 8514, 500 ASA) providing high resolution. However, problems with light striking the film during loading and unloading the camera limited the useable photographs to a period from 6 March to 6 June 1991.

Oblique photographs taken with the free-vehicle camera were analysed using a perspective grid method (Wolf, 1983; Wakefield and Genin, 1987). Each film image was projected onto a flat surface and digitized with an electronic digitizer (Science Accessories Corp.) interfaced with a computer. A computer program was developed in our laboratory

Table 1. *Time-lapse camera deployments to examine features and processes associated with the sea floor in soft-substrate environments. Only studies with measurement durations of* >0.5 day *are included. Camera type: motion picture (m), still (s), video (v). Camera orientation: vertical (v), oblique (o). *Published as* 20 m^2 *but more recently corrected to* 8.9 m^2 *(I. G. PRIEDE, personal communication)*

Location	Depth (m)	Camera type	Camera orientation	Film (mm)	Area photographed (m^2)	Exposure interval (min)	Duration of measurements (day)
Central N. Pacific	5304	s	v	35	?	10	0.8
NW Atlantic	360	m	o	16	1	4.3	1.8
W. Pacific	5861–9806	s	o & v	35	?	5	≤1.2
E. tropical Pacific	4873	s	o	35	1	240	202
NW Atlantic	60–87	s	v	35	2.2	120	14–68
Bering Sea	18	s	v	35	?	120–240	20
Straits of Florida	710	m			1.4	60	43
NE Atlantic	2000	s	o	35	2	60	33
NE Atlantic	5300	s	o	16	0.6	64	64
NE Atlantic	2664	s	o	35	2	16	8.9
E. tropical Pacific	3587–4906	s	o & v	35	0.9–1.7	120–240	123–395
NE Pacific	3800–5800	v	o		4	0–30	≤0.6
NE Atlantic	512–4101	s	o	35	2	4–512	0.5–104
NE Pacific	1310	s	v	35	0.9	60–120	4–57
NE Atlantic	4100	s	o	35	4.8	64	32
NW Atlantic	22	s	o	8	1.5	30	15
NE Pacific	90	s	v	35	1.7	120–240	≤90
NW Atlantic	4800	s	v	35	0.4	60	113
NE Pacific	1300	s	v	35	0.9	60	42
NE Pacific	4400–5900	v	o		8.9*	0–15	≤0.9
NE Pacific	90	s	v	35	0.3	12	90

No. deployments	Other attached instruments	Emphasis of study	Reference
1	none	biological activity, disturbance (bait)	HESSLER *et al.* (1972)
1	none	biological activity	ROWE *et al.* (1974)
?	none	biological activity, disturbance (bait)	HESSLER *et al.* (1978)
1	nephelometer, current meter	biological activity	PAUL *et al.* (1978)
5	transmissometer, current meter	sediment transport, near-bottom currents	BUTMAN *et al.* (1979)
1	current meters, pressure/ temp. sensor, nephelometer/ transmissometer	sediment transport, near-bottom currents	CACCHIONE and DRAKE (1979)
1	current meter	sediment transport, near-bottom currents	WIMBUSH and LESHT (1979)
1	current meter	sedimentation (POM)	BILLETT *et al.* (1983)
1	current meter	near-bottom currents/temperature	ELLIOTT and THORPE (1983)
1	current meter	biological activity	LAMPITT and BURNHAM (1983)
5	current meter, nephelometer	near-bottom currents, suspended particulates, biological activity	GARDNER *et al.* (1984)
10	none	biological activity, disturbance (bait)	WILSON and SMITH (1984)
16	current meter	sedimentation (POM), biological activity	LAMPITT (1985)
3	none	biological activity, disturbance (bait)	SMITH (1985)
1	current meter	biological activity	LAMPITT and PATERSON (1987)
1	transmissometer, current meter, sonar, pressure sensor	sediment transport, near-bottom currents	AMOS *et al.* (1988)
2	current meter, pressure/temp. sensor, nephelometer/ transmissometer	biological activity	NICHOLS *et al.* (1989)
1	?	biological activity	WHEATCROFT *et al.* (1989)
1	none	biological activity	WHEATCROFT *et al.* (1989)
29	acoustic tracking	biological activity, disturbance (bait)	PRIEDE *et al.* (1990)
1	none	sediment transport, bottom roughness	WHEATCROFT (in press)

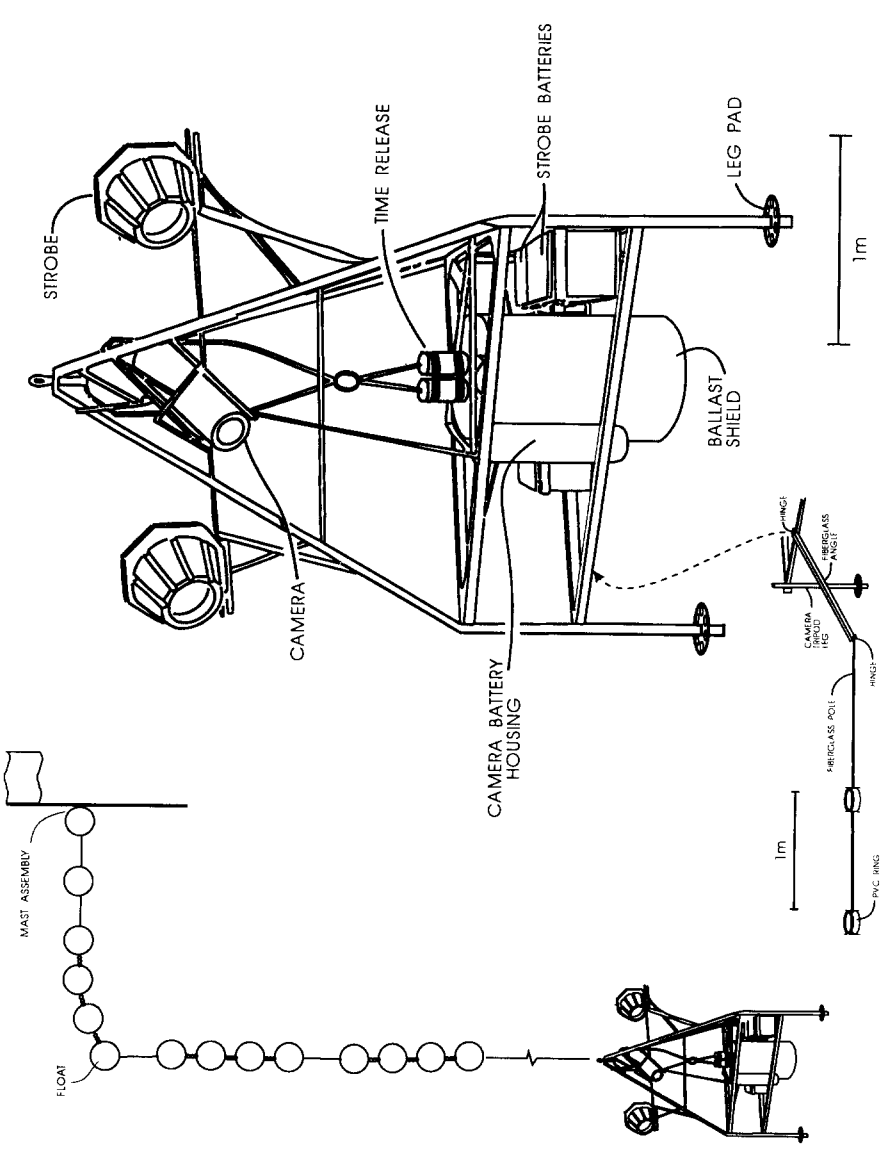

Fig. 1. The free-vehicle time-lapse camera system illustrating the camera tripod with component parts, the field marker assembly and the overall configuration of the camera system deployed as a free vehicle, including flotation.

to measure the lengths and areas of objects on the sea floor using this system (WAKEFIELD and GENIN, 1987). The field marker served as a check that the geometry of the camera (elevation and inclination) was maintained on the sea floor and that the dimensions of the perspective grid were accurate with a maximum resolution of 3 mm on the X axis and 5 mm on the Y axis.

Digitized data were analysed by treating sequential photographs as serial observations of a semicircular area with the camera at its center. Data of this type can be treated using techniques similar to those developed for the censusing of birds by a single stationary observer (see review by BUCKLAND *et al.*, in press). Radial distances from the camera were computed for each organism observed, then a probability density function was fitted to the observed distribution of distances, using the computer program DISTANCE (LAAKE *et al.*, 1991). In this case, the probability density function represents the probability of an observer detecting an object located a given distance away. Integrating this function for a given type of object yielded an effective observation area; this effective area was used in combination with the number of objects detected to generate an estimate of object density (RAMSEY and SCOTT, 1979).

The area of the sea floor over which the megafauna were visible was species-specific and depended primarily on the size, color and posture of the animal with respect to the sediment (KAUFMANN *et al.*, 1989). In general, species that were translucent or whose color closely resembled that of the surrounding sediment were difficult to discern in areas of suboptimal lighting (close foreground and distant background), while organisms whose color or texture contrasted markedly with that of the sediment were identifiable over a much larger area. This area ranged from 4.9 m^2 for rare, sediment-colored holothuroids to 26.6 m^2 for large transparent holothuroids elevated above the sediment surface on podia (*Oneirophanta mutabilis*). Because of the variation in area over which different species could be detected, we normalized all species densities to a 20 m^2 area for comparative purposes. These density estimates include animals observed in hourly photographs with no attempt to identify presence or absence of specific individuals between frames.

Representative specimens of epibenthic megafauna were collected at the beginning and end of the time-lapse camera deployment with a semi-balloon trawl (5-m foot rope; 3.8-cm stretch mesh with 1.3-cm mesh cod-end liner). These specimens were preserved in 10% formalin, identified by appropriate specialists, and then used in tentative identifications of the animals in the time-lapse photographs. We stress that the identifications of animals in the photographs are tentative and are subject to error since the actual specimens in the photographs were not collected.

A sediment trap array was deployed concurrently with the camera system to collect particulate matter sinking through the benthic boundary layer at 50 m above bottom (mab) as part of a long time-series program at this station (SMITH *et al.*, 1992). The sediment trap consisted of a steep-sided cone with a mouth opening of 0.25 m^2 and a baffle to reduce turbulence (BRULAND *et al.*, 1981). A sequencer mounted on the bottom of the cone (HONJO and DOHERTY, 1988) was set to collect the sedimenting particles for 12 10-day periods from 25 February to 25 June 1991. The collection cups were filled prior to deployment with water obtained from the collection depth and filtered through pre-combusted GF/C filters. Each collection cup was then poisoned with filtered $HgCl_2$ (3.0 mM final concentration). On recovery of the sediment traps, "swimmers" were removed and the remaining sample resuspended and split into four equal-volume aliquots. Three aliquots were frozen (−70°C) for laboratory analysis while a fourth was preserved for

microscopic analysis. One frozen aliquot from each collection cup was thawed, centrifuged, the supernatant decanted and the remainder lyophilized, weighed and ground to a fine powder. These samples were then analysed in duplicate for total carbon using a Perkin–Elmer 2400C elemental analyser and particulate inorganic carbon using a Coulometrics carbon analyser. Organic carbon was determined by difference between the total and inorganic carbon (REIMERS and SMITH, 1986), with correction for salt content using $AgNo_3$ titration (STRICKLAND and PARSONS, 1972). Another frozen aliquot from each collection cup was thawed, centrifuged, extracted in 90% acetone and analysed for chlorophyll *a* and phaeopigments (PARSONS *et al.*, 1984). We report here only the organic carbon and chlorophyll *a* determinations.

RESULTS

The sea floor in the study area is characterized by silty-clay sediments with little relief over extensive areas (<60 m relief over 770 km^2). On smaller spatial scales there are small mounds and depressions on the scale of centimeters and occasional large mounds on the scale of decimeters. Protruding from the sediment surface are numerous tubes of the polychaete, *Paradiopatra* sp. (Family Onuphidae). Small depressions (<4 cm dia.) dominate the sediment surface. These depressions are generally formed by ophiuroids which frequently undergo vertical excursions to the sediment surface and often leave their arms extended above the sediment while the disk is submerged. The dominant ophiuroid recovered in trawls was *Ophiura bathybia*, with smaller numbers of *Amphilepis patens*, *Amphiura carchara* and *Ophiacantha* sp. We rarely observed these species moving laterally across the sediment surface, and they were often submerged in the sediment, making their density difficult to quantify. Hence, ophiuroids were not considered in the following analysis of the mobile megafauna, which we define here as those animals detectable in bottom photographs and exhibiting discernible horizontal movements across the sediment surface.

The total density of the mobile megafauna, excluding ophiuroids, was episodic over the 3-month period, and daily means ranged from 0 to 13.6 animals $(20\ m^2)^{-1}$ (Fig. 2a), equivalent to 0–680 individuals $(10^3\ m^2)^{-1}$. These megafaunal density estimates at Sta. M fell within the range for total megafauna (2–3500 animals $(10^3\ m^2)^{-1}$ measured in other studies covering larger areas of the sea floor using trawls and camera systems over depths between 3000 and 5000 m in the North Atlantic (MAUVIEL and SIBUET, 1985; OWEN *et al.*, 1967; SIBUET *et al.*, 1984; SIBUET and SEGONZAC, 1985), North Pacific (PAWSON, 1988; SMITH, 1992), Arctic and Southern Oceans (KITCHELL *et al.*, 1978). The highest peak in mobile megafaunal density at Sta. M immediately preceded initial increases in the fluxes of POC and chlorophyll *a* at 50 m above bottom (Fig. 2b).

The mobile epibenthic megafauna were dominated numerically by the holothuroids, *Abyssocucumis abyssorum*, *Peniagone vitrea* and *Elpidia minutissima*. Less common species included the holothuroid, *Oneirophanta mutabilis*, and the echinoid, *Echinocrepis* sp. *Abyssocucumis* was present in early March and then reappeared in late May, while *Peniagone* was sporadically present throughout the camera deployment but was most prevalent in late March and April (Fig. 2c). *Elpidia* made sporadic appearances until mid April, when a peak in density occurred followed by secondary peaks in May and June. The peak in density of *E. minutissima* coincided with the peak in total megafaunal density (Fig. 2a).

The distances traversed by five species of megafauna were highly variable (Table 2) but fell within the range of crawling rates summarized for various deep-sea megafauna (6–462 cm h^{-1}; WHEATCROFT *et al.*, 1989). The slowest species we recorded was *Echinocrepis* (8.1 ± 7.9 cm h^{-1}), which frequently stopped while slowly plowing a deep furrow through the surface sediment. In contrast, *Oneirophanta mutabilis* moved rapidly across the field of view, leaving no visible trace and recording the fastest speed for the megafauna (84.8 ± 80.9 cm h^{-1}). The other three species, *Abyssocucumis*, *Peniagone* and *Elpidia*, exhibited a different behavior, making short excursions interrupted frequently by bouts of localized, closely-spaced turns ("milling" activity).

We mapped the movements of the mobile megafauna at hourly intervals during each of the three months from 6 March to 6 June (Fig. 3). These movements were only recorded for animals that remained in the field of view for two or more contiguous photographs. Over the 3-month period, much of the sediment surface was covered by the movements of the megafauna, especially within 400 cm of the baseline of the frame, beyond which the smaller animals (e.g. *Elpidia minutissima*) were not visible. Our estimates of the paths traversed by these species are minimal, since they only represent the net movement between positions observed hourly. The slow plowing movements of *Echinocrepis* were primarily evident in March–April (Fig. 3a; overlapping triangular pattern), while the "hot spots" of activity created by the "milling" pattern of *Abyssocucumis*, *Peniagone* and *Elpidia* were more apparent in April–May (Fig. 3b) and May–June (Fig. 3c).

The total area traversed by the megafauna each day was estimated by measuring the distance traveled by each animal between hourly photographs and multiplying that distance by the animal's body width, then summing the areas for all animals moving on a given day (Fig. 2d). Area traversed by the megafauna was highly variable on a daily basis but ranged from 0 to a high of 7691 cm^2 in early May. The peak in area traversed occurred several weeks after the primary peak in megafaunal density during mid-April (Fig. 2a). Although the per cent area traversed by the megafauna was ≤3.9% of the 20 m^2 surveyed per day, integration of area traversed for the 3-month period yielded a total area of 17.6 m^2 or 88% of the surveyed area of sea floor. This estimate of the sea floor impacted by the mobile megafauna does not include areas traversed more than once and underestimates the distance traveled between hourly photographs. However, even with these biases, it is obvious from the monthly tracking of these animals (Fig. 3) that the mobile megafauna traversed a considerable portion of the sea floor.

DISCUSSION

The area influenced by the mobile megafauna was species-specific. The dominant holothuroids, *Abyssocucumis abyssorum*, *Peniagone vitrea* and *Elpidia minutissima*, left little visual trace on the sediment surface whereas the rare echinoid, *Echinocrepis* sp., bulldozed the sediment surface, leaving a pronounced furrow in the sediment. WHEATCROFT *et al.* (1989) proposed that the trace-producing potential of mobile megafauna was related to animal size, mechanics of locomotion and microscale sediment roughness. Based on sediment roughness, they classified holothuroids as "contingent trace producers" while echinoids were "obligate trace producers", in agreement with our findings. At our study site, the "contingent trace producers" did not typically produce traces, with little evidence of destruction of previous traces. These organisms probably generate traces

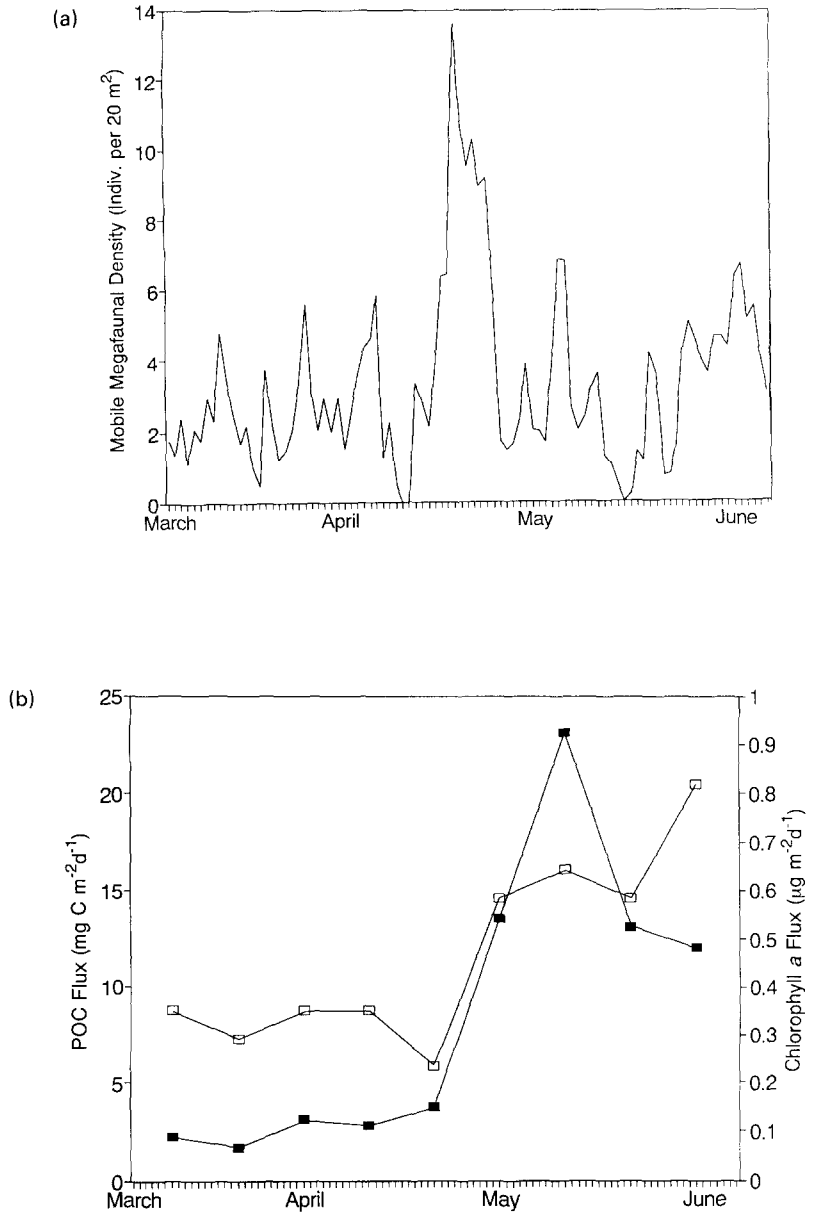

Fig. 2. Mobile megafaunal density and area traversed in the field of view of the time-lapse camera compared to the POC flux over a 3-month period from 6 March to 6 June 1991 at an abyssal station in the eastern North Pacific (Sta. M). (a) Density of mobile megafauna, excluding ophiuroids, computed as a daily mean from hourly photographs. (b) POC (solid boxes) fluxes measured in duplicate and chlorophyll *a* (open boxes) fluxes measured at 10-day intervals 50 m above the sea floor (symbols represent midpoints of 10-day sampling intervals; duplicate values fall within the borders of the boxes). (c) Density of the three dominant holothuroids, *Abyssocucumis abyssorum* (solid line), *Peniagone vitrea* (dashed line), and *Elpidia minutissima* (dotted line), computed as daily means from hourly photographs. (d) Area traversed by the mobile megafauna each day (see text). Solid line represents total area; dashed line depicts area per mobile animal observed.

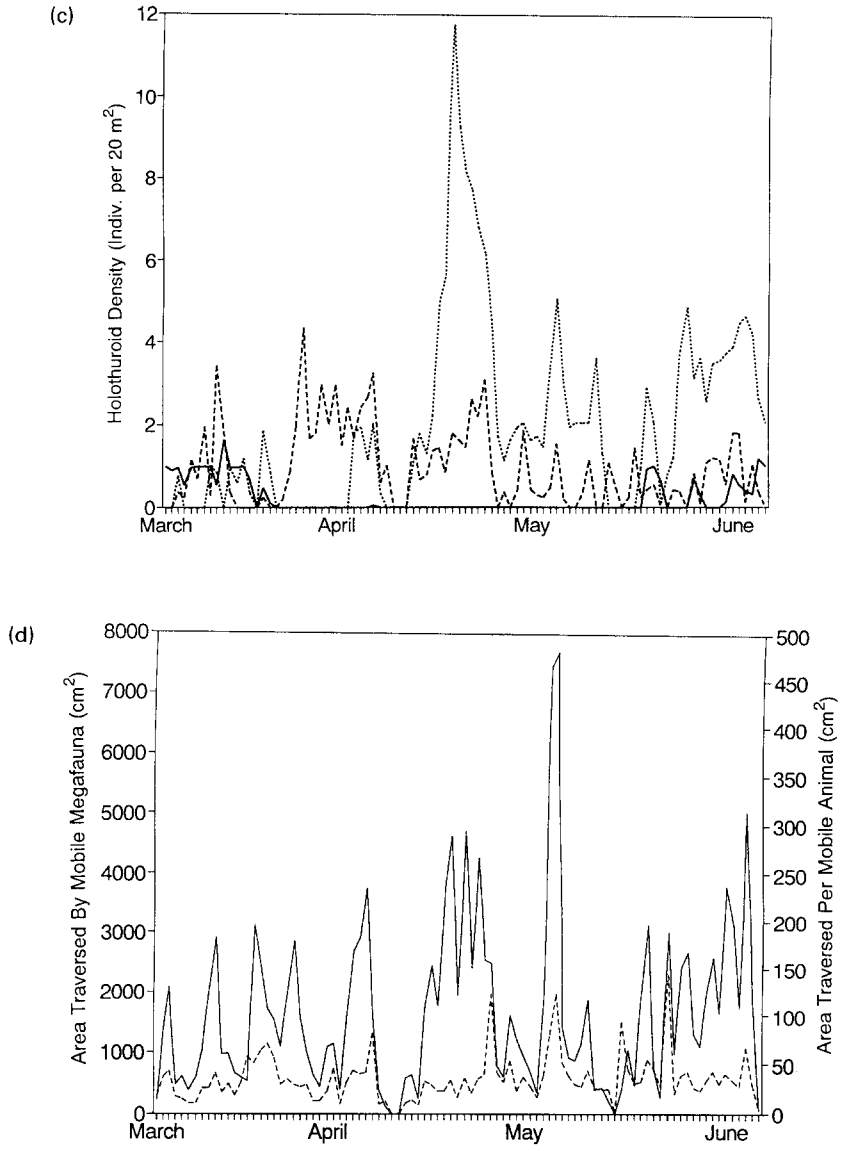

Fig. 2 (c),(d).

on a spatial scale smaller than that characteristic of the sediment surface, rendering them virtually invisible against the ambient background (WHEATCROFT *et al.*, 1989).

Regardless of whether animals produce traces in the sediment, the foraging of these deposit-feeding megafauna on surface organic material and their production of mucus and fecal material all impact the areas traversed. We contend that the area traversed by the mobile megafauna was altered by their presence, ultimately affecting biological and chemical processes in the sediment. Hence, in a 3-month period, the majority of the sediment surface (*ca* 88%) was impacted by the mobile megafauna. Our results show an increase in the daily area traversed by the mobile megafauna coincident with an increase in

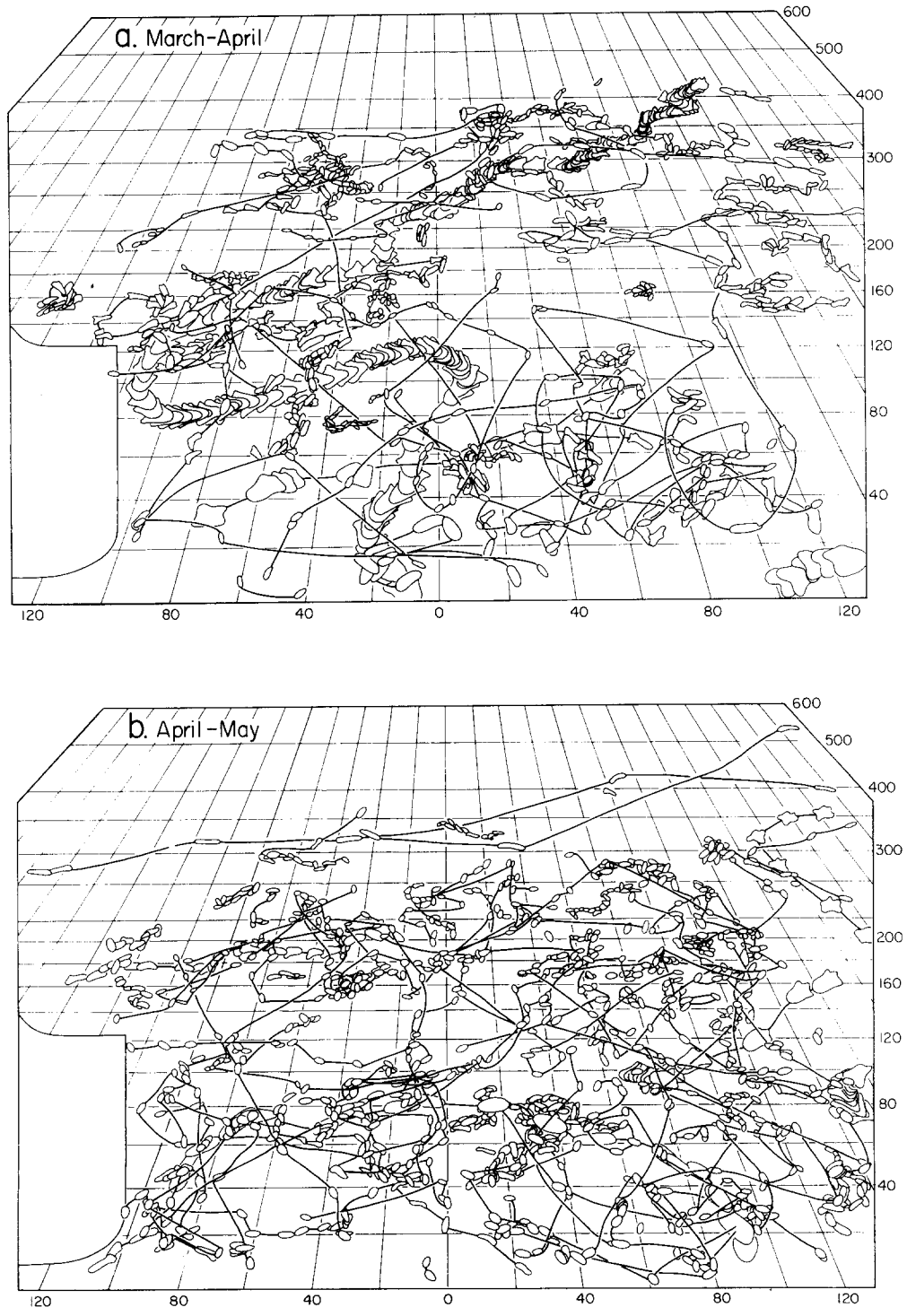
a. March-April
600
500
400
300
200
160
120
80
40
120
80
40
0
40
80
120
b. April-May
600
500
400
300
200
160
120
80
40
120
80
40
0
40
80
120

Fig. 3 (a),(b).

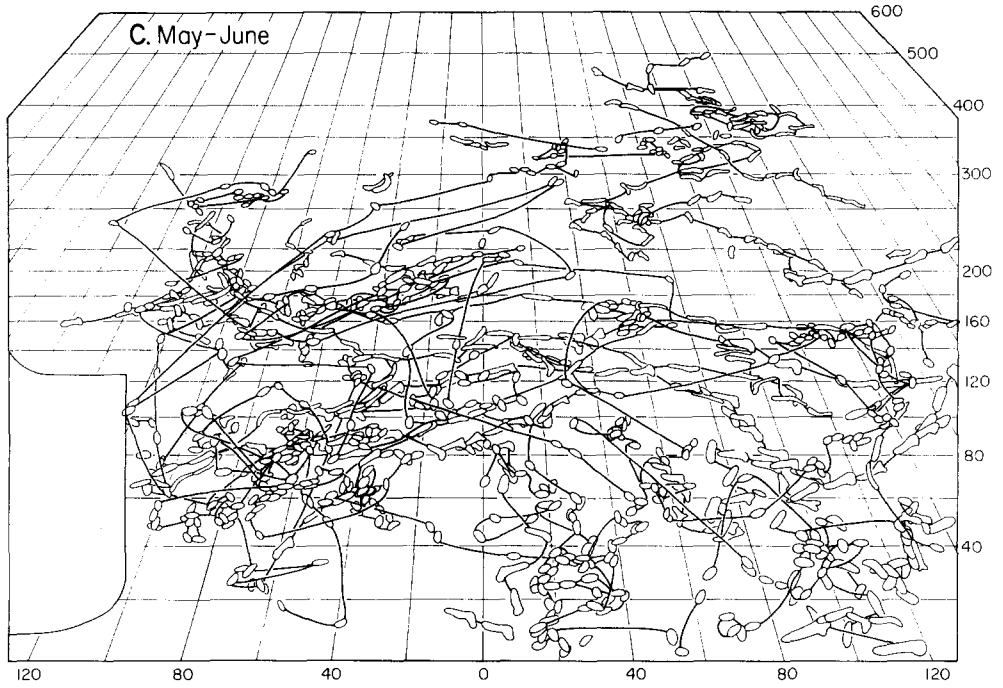

Fig. 3. Movements of the mobile megafauna depicted for three months, (a) 6 March – 6 April, (b) 6 April – 6 May and (c) 6 May – 6 June 1991 at Sta. M. The perspective grid is labelled with distances (cm) from the origin and baseline of the photograph. The data chamber window which appears in each photograph is shown as a blank area to the left. The shape of each animal is outlined every hour (e.g. the triangular shape represents the echinoid, *Echinocrepis* sp., the elongate ovals are the holothuroid, *Abyssocucumis abyssorum*, and the L-shapes are the holothuroid, *Peniagone vitrea*). Lines connecting the shapes of each animal represent the estimated path traversed between hourly photographs.

the input of organic matter from the overlying water during this period, implying that their activity was related to foraging for food. Some holothuroids selectively feed on sediment particles of higher nutritive value than those found in the surrounding sediment at abyssal depths (KHRIPOUNOFF and SIBUET, 1980). Selective feeding by deep-sea holothuroids on freshly deposited chlorophyll (BILLETT *et al.*, 1988) and amino acids (ALBERIC and KHRIPOUNOFF, 1984) also has been reported.

We made some simple calculations to estimate the potential importance of the mobile megafauna in the processing or mineralization of the organic carbon entering the benthic boundary layer at Sta. M. During the period from March to June 1991, the sinking POC flux was generally composed of small particles that were not visible as detrital aggregates in our photographs of the sea floor. If we assume that the POC flux measured at 50 mab with 10-day resolution arrived on the sea floor within one day (assuming all three conditions) was evenly dispersed over the sediment surface, and that the particles on areas of sea floor traversed by the megafauna were ingested during the same period, then simple calculations can be made concerning the impact of the mobile megafauna on carbon cycling. Over the 90 days covered by this time series, the POC flux ranged from 0.33 g C $(20\ m^2)^{-1}$ (10-day mean) in March to a high of 4.6 g C $(20\ m^2)^{-1}$ (10-day mean) in May, totalling

*Table 2. Body size and hourly distance traversed by five species of mobile megafauna estimated from time-lapse photographs taken at Sta. M from March to June 1991. The number of measurements of body size and distance traversed were made on all animals present in each photograph taken hourly. *The base of these animals resembled an equilateral triangle and hence only one dimension is given*

	Body size					Distance traversed hourly (cm)		
	Length (cm)		Width (cm)					
Species	Mean ± S.D.	Range	Mean ± S.D.	Range	No.	Mean ± S.D.	Range	No.
Holothuroidea								
Abyssocucumis abyssorum	9.7 ± 2.1	3.1–16.9	3.1 ± 0.9	1.0–9.0	476	17.8 ± 13.4	1.9–63.3	155
Peniagone vitrea	7.3 ± 2.1	1.9–16.9	2.7 ± 0.9	0.9–8.0	1458	8.1 ± 7.9	0.6–110.0	1010
Elpidia minutissima	4.1 ± 0.9	1.7–8.6	2.3 ± 0.7	0.9–6.0	2134	14.8 ± 15.3	0.5–129.8	1207
Oneirophanta mutabilis	14.3 ± 1.6	11.5–17.4	3.8 ± 1.7	1.3–6.9	14	84.8 ± 80.9	10.1–277.4	11
Echinoidea								
Echinocrepis sp.*	9.6 ± 1.3	6.5–12.9			279	6.2 ± 7.0	0.8–48.1	216

15.03 g C over the 20 m^2 study area for 90 days. Over the same 10-day periods, the mobile megafauna traversed between 5.18% of the study area in early April and 15.19% in mid April. Multiplying the traversed area by the POC flux for each 10-day period and then summing the nine periods yielded an estimate of 1.31 g C ingested by the mobile megafauna, amounting to 8.7% of the available POC in a 20 m^2 area.

Given the organic carbon ingested by the mobile megafauna, we estimated how much of this material would be assimilated and metabolized to CO_2, leaving the remainder modified as fecal material. To make these calculations, three parameters were needed: the density, size and oxygen consumption for the dominant megafaunal species. For simplicity, we limited these calculations to the two dominant species of mobile megafauna observed during the three-month sampling period, *Elpidia minutissima* and *Peniagone vitrea* (Fig. 2c).

The densities of *Elpidia* and *Peniagone* were estimated by integrating the curves representing their daily abundances over the sampling period (Fig. 2c), yielding values of 194.1 and 92.3 individuals $(20\ m^2)^{-1}$, respectively. It must be emphasized that these estimates represent independent sightings but not different animals, since often the same animal was observed over periods >1 day. Combined, these two species of holothuroids comprised 87.4% of the total mobile megafauna during the three-month observation period [327.7 individuals $(20\ m^2)^{-1}$, derived by integration of the curve in Fig. 2a].

Length and width of each dominant species are given in Table 2. We took the mean dimensions, assuming each individual to be a cylinder, and computed a volume of 17 cm^3 for *E. minutissima* and 41.8 cm^3 for *P. vitrea*. Both of these species had a high water content (>90% water, SMITH, unpublished data), justifying the use of the density of seawater to yield a mean animal wet weight of 17.5 g for *E. minutissima* and 43.1 g for *P. vitrea*. We used a regression of weight-specific oxygen consumption as a function of wet weight derived from *in situ* rates measured for smaller individuals (<10 g wet weight) of a similar species, *Scotoplanes globosa*, at 1300 m (SMITH, 1983), to estimate the oxygen

consumption for *E. minutissima* and *P. vitrea*: 3.45 μl O_2 (g wet wt)$^{-1}$ h^{-1} and 2.61 μl O_2 (g wet wt)$^{-1}$ h^{-1}, respectively. These respiration rates were converted to carbon, assuming a respiratory quotient of 0.85 (mixed carbohydrate and lipid; BRODY, 1945), and then multiplied by the number of individuals for each species to yield a population carbon consumption of 129.4 mg C (20 m^2)$^{-1}$ for *E. minutissima* and 114.2 mg C (20 m^2)$^{-1}$ for *P. vitrea*.

The estimated carbon demand by the mobile epibenthic megafauna was thus 0.24 g C (20 m^2)$^{-1}$ over the 3-month period, representing 18.3% of the estimated organic carbon ingested by these deposit-feeding holothuroids. Hence, 81.7% of the estimated organic carbon ingested by the mobile megafauna should have been egested as fecal material. KHRIPOUNOFF and SIBUET (1980) estimated that deposit-feeding holothuroids assimilated 15% of the ingested organic carbon from surface sediment in the Bay of Biscay (2000–4500 m depth). Their estimate of assimilation closely agrees with our respiration-based estimate of 18.3%, if we assume that all the carbon assimilated was utilized in catabolic processes with no growth. Similarly, SIBUET (1988 cited in BILLETT, 1991) reported that holothuroids utilized approximately 20% of the organic matter reaching the sea floor at bathyal depths.

From a different perspective we compared the estimated mineralization of organic carbon by the mobile megafauna with the POC flux at this station for the same period of time. The mobile megafauna consumed only 1.6% of the POC flux [15.03 g C (20 m^2)$^{-1}$] measured at 50 mab over this same period. Even if the other 12.6% of the mobile megafauna were included in this estimate and active rates of metabolism were considered in our calculations, we doubt if this consumption rate would increase more than 100%, still leaving the mobile megafauna as minor consumers of organic carbon. In the eastern North Atlantic, LAMPITT *et al.* (1986) estimated that the megafauna required 1% of the POC flux, based on calculations using a regression analysis of primary productivity and depth (SUESS, 1980). These findings are in contrast to the more oligotrophic central North Pacific, where the epibenthic megafauna were estimated to be proportionately more important as consumers of organic carbon (SMITH, 1992), metabolizing 7–50% of the POC flux entering the benthic boundary layer.

Although the epibenthic megafauna apparently contributed little to the direct mineralization of organic carbon at Sta. M, it should be noted that they did traverse a substantial proportion of the sea floor. Because of this extensive coverage, it seems likely that these animals are important as modifiers of the surface sediments, either through mixing (*cf.* WHEATCROFT, 1991) or repackaging of organic material for mineralization by the sediment community.

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