

5-1997

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Publication Info

Published in *Limnology and Oceanography*, Volume 42, Issue 3, 1997, pages 589-595.

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Submitted: 22 January 1996
Accepted: 29 September 1996
Amended: 29 January 1997

Limnol. Oceanogr., 42(3), 1997, 589–595
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Abstract—Particle-scavenged ^{234}Th and ^{210}Pb can be used to trace the fate of particulate matter reaching the deep-sea floor. We used this technique to demonstrate rapid ingestion of particles arriving at the sea floor (at a depth of 4,100 m) by mobile epibenthic holothuroids (*Abyssocucumis abyssorum* and *Oneirophanta mutabilis*). Excess ^{234}Th and ^{210}Pb activities of sediment trap material, detrital aggregates from the sea floor, and animal gut contents all were similar while activities of surface sediments (top 0–5 mm) were considerably lower. A simple calculation using the excess ^{210}Pb concentration of two potential food sources, sediment trap material and surface sediments, shows that ~91% of gut content material of *A. abyssorum* must have come from material similar to that found in the sediment trap cups. By setting the sediment trap material as age 0, apparent ages of <0–20 d, >100 d, and 12–13 d were estimated for the aggregates, surface sediments, and *A. abyssorum* guts, respectively. The population of *A. abyssorum* at this site could potentially process 0.2–4% of the vertical mass flux ($\text{m}^{-2} \text{d}^{-1}$) during the high particle flux period between June and October 1994. The percentage of vertical flux processed could be substantially greater when all of the mobile epibenthic megafauna species are considered.

Biological processes have an important role in determining the degree of recycling or burial of particles reaching the deep-sea floor. Pelagic–benthic coupling between settling particles and microbial and infaunal components of the abyssal benthos has been documented by measurements of sediment community oxygen consumption (Jahnke and Jackson 1987; Smith et al. 1994), ATP content (Linke 1992; Smith et al. 1994), and growth rates of bacteria and protozoa (Goody and Turley 1990). Much less is known about the degree of trophic coupling between settling material and the larger fauna living on the abyssal sediment surface. Only a few bioturbation studies (e.g. Wheatcroft 1991; Hoover and Smith unpubl.), several reports of large epibenthic animals feeding on fresh detrital material (e.g. Billett et al. 1988; Pfannkuche and Lochte 1993), and several studies of mega-

faunal activity and respiration rates (e.g. LaFonde 1967; Smith 1983; K. L. Smith et al. 1993) address the potential role of mobile epibenthic megafauna in determining the fate of sinking particles.

Epibenthic megafauna (animals living on the sediment surface and large enough to be visible in photographs) generally are not as abundant as their smaller infaunal counterparts and often are not considered in studies of deep-sea sediment processes. However, many epibenthic megafauna are surface deposit and/or suspension feeders, and adaptations for particle selection often are associated with such feeding modes (Gage and Tyler 1991). The mobility of many of these species adds the potential for redistributing recently settled material horizontally over the sediment surface (K. L. Smith et al. 1993). Photosynthetic pigments have been used successfully to trace large seasonal inputs of food from surface waters into the guts of abyssal holothuroids (Billett et al. 1988; Pfannkuche and Lochte 1993). However, quantifying the role of these animals in the fate of settling particles has proved difficult. Naturally occurring tracers such as radionuclides, used previously in radioecological studies in both pelagic waters (Heyraud et al. 1988) and the deep benthos (Feldt et al. 1985; C. R. Smith et al. 1993), provide a powerful technique for quantifying the contribution of mobile epibenthic megafauna to sediment processes.

Ingestion of particulate matter by benthic organisms can be traced using the naturally occurring radionuclides ^{234}Th and ^{210}Pb , which are strongly adsorbed by particles (Aller and DeMaster 1984; Moore and Dymond 1988). ^{234}Th , produced throughout the water column by ^{238}U decay and scavenged by sinking particles, has a short half-life (24.1 d) and therefore is a very useful identifier of newly settled particles (100-d time scales). ^{210}Pb , supplied by in situ production from ^{226}Ra and atmospheric input, has a long half-life (22.3 yr) relative to ^{234}Th . ^{210}Pb is used to track particles on the order of 100 yr and is essentially stable over the time scales relevant to this study. To account for any possible fraction-

Table 1. Mean activities of excess ^{234}Th and ^{210}Pb (in disintegrations per minute per gram dry weight) and mean apparent ages (in d) of four sample types. Ages are relative to sediment trap samples with defined age = 0.

Sample type	Mean \pm SD excess ^{234}Th	Mean \pm SD excess ^{210}Pb	Mean apparent age
50 mab sediment trap samples ($n = 9$)	2,990 \pm 560	262 \pm 50	0
Detrital aggregates A ($n = 2$)	272 \pm 30	44 \pm 2	20
Detrital aggregates B ($n = 3$)	2,050 \pm 660	172 \pm 56	<0
Surficial sediments 0–2.5 mm ($n = 6$)	19 \pm 14	57 \pm 9	>100
Surficial sediments 2.5–5 mm ($n = 5$)	11 \pm 6	52 \pm 4	>100
<i>Abyssoicum abyssorum</i> foreguts ($n = 5$)	1,900 \pm 610	244 \pm 41	13
<i>A. abyssorum</i> hindguts ($n = 9$)	1,370 \pm 580	166 \pm 63	12

ation due to compositional or grain size changes, we used excess (unsupported by decay of parent radionuclide) ^{210}Pb activity to normalize excess ^{234}Th activity. We then used the ^{210}Pb : ^{234}Th activity ratio to calculate apparent age differences between particulate matter from the water column and particles extracted from digestive tracts of epibenthic animals. Such ages indicate whether organisms utilize freshly settled (^{234}Th -rich) or older (^{234}Th -poor) particles.

Using this approach, we compared ages of a variety of particulate samples collected in the water column and on the sea floor at a single abyssal site (Sta. M; 4,100-m depth at 34°50'N, 123°00'W) between June and October 1994. Station M is characterized by seasonal increases in particle flux to the benthos and the appearance of visible patches of detrital material on the sediment surface during summer and fall (Smith et al. 1994; Lauerman et al. 1996). Our collections in August and September coincided with a high flux period when detrital material in the form of a fluff layer and discrete aggregates was visible on the bottom (R. J. Baldwin in prep.).

We measured excess ^{234}Th and ^{210}Pb activities of four sample types to determine if mobile epibenthic animals are selective feeders, discriminately ingesting recently settled particles. As potential food sources, we collected and measured radionuclide activities of sedimenting particulate matter, detrital aggregates, and surface sediments. The activities of these samples were compared to activities of animal gut contents.

Sinking particulate matter was collected in sediment traps (Smith et al. 1994) with 10-d resolution moored at 50 m above bottom (mab) between June and October 1994. Cups were filled prior to each deployment with water that was collected at deployment depth, filtered with combusted GF/C filters, and poisoned with HgCl_2 (3.0 mM final concn). On recovery of the sediment traps, "swimmers" were removed and the samples were frozen at -70°C . In the laboratory, samples were thawed, centrifuged, and the particulate matter was then lyophilized and ground following the protocol of Smith et al. (1994).

Detrital aggregates and surface sediments were collected in acrylic tube cores (7 cm diam \times 20 cm long) with the submersible *Alvin* during August and September 1994. These tube cores were equipped with flapper valves to minimize the effects of bow waves on the enclosed samples. Upon recovery of the submersible, tube cores were trans-

ferred to a refrigerated van (2°C) for processing. After siphoning off most of the top water, detrital aggregates were carefully removed from cores; wide bore pipettes were used to minimize contamination from surface sediments. Aggregates were stored frozen (-70°C) in filtered seawater until processed. One set of detrital aggregates (Table 1; A, $n = 2$) was dried down in a small volume of seawater, resulting in high salt concentrations; the others (Table 1; B, $n = 3$) were centrifuged and the pellet dried (same protocol used for sediment trap samples), eliminating much of the salt. Sediment cores were sectioned in 2.5-mm increments to a depth of 2 cm and in 0.5-cm sections from 2 to 4 cm. The resulting samples were dried and ground. The top two sections (0–2.5 mm, 2.5–5 mm) were analyzed for radionuclide activity.

Epibenthic megafauna were collected with a semiballoon trawl (5-m foot rope; 3.8-cm stretch mesh with 1.3-cm-mesh cod-end liner) trailing a camera sled. Some specimens were preserved in 10% formalin; others were immediately frozen in liquid N_2 and later transferred to a -70°C freezer until processing. We later extracted gut contents from the dendrochirotid holothuroid *Abyssoicum abyssorum* and the elapsidid holothuroid *Oneirophanta mutabilis*. Foregut material was extracted from the muscular pharyngeal bulb and hindgut material from the long coiled digestive tract. Both species, like most deep-sea holothuroids, are considered deposit feeders (Gage and Tyler 1991), and *A. abyssorum*, like its shallow-water relatives, may suspension feed as well (pers. obs.; Barnes 1980).

All samples were dried and weighed, and mass values were corrected with a salt factor measured by a variation of the Mohr–Knudsen titration (Grasshoff 1983). Weighed fractions of each sample were packed into 3-dram (20-ml) vials for radioisotope counting. Gamma ray spectrometry with an intrinsic well germanium detector was used to determine the activities of ^{234}Th and ^{210}Pb (Moore 1984; Thunell et al. 1994). The measured activities were converted to disintegrations per minute per gram using liquid standards measured in the same geometry. The self-absorption coefficients of the materials lightly packed in the counting vials were within a few percent of that of water, therefore additional self-absorption corrections were not necessary. ^{234}Th activities were corrected for decay since the midpoint of the 10-d collection period for sediment trap samples and since the time of collection for all other samples.

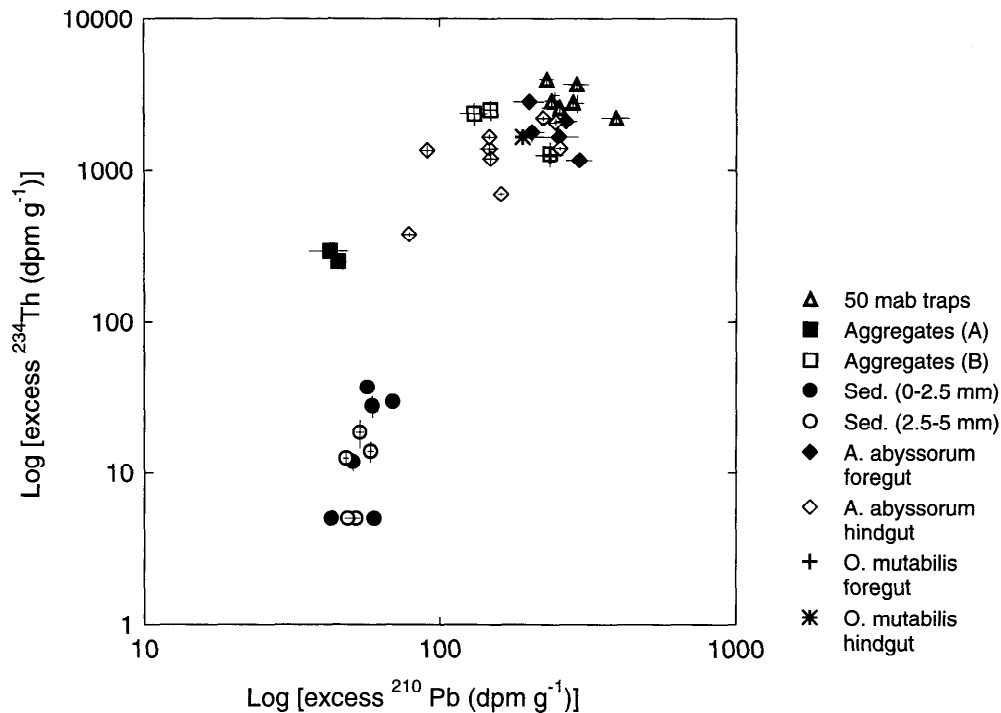


Fig. 1. Log-log plot of excess ^{210}Pb vs. ^{234}Th activity of sediment trap material, detrital aggregates, surface sediments, and animal gut contents collected at Sta. M between June and October 1994. For all samples excluding surface sediments, masses were small and only material for which both ^{210}Pb and ^{234}Th activities were detected have been plotted. The surface sediment masses were all large and contained ample ^{210}Pb , so lack of ^{234}Th probably was not an artifact of small sample size. A threshold ^{234}Th value of 5 dpm (gDW)^{-1} was assigned to those sediment samples with ^{234}Th activities below the detection limit of the gamma spectrometer [5 dpm (gDW)^{-1}] in order to make these data visible in the figure. One set of detrital aggregates (A, $n = 2$) was dried down in a small volume of seawater, resulting in high salt concentrations; the others (B, $n = 3$) were centrifuged and the pellet dried, eliminating much of the salt. Error bars represent the statistical counting error of the spectrometer.

Two potential food sources for mobile epibenthic megafauna—sediment trap material and surface sediments—have different but constant (on short time scales) excess ^{210}Pb signatures. By measuring the excess ^{210}Pb activities of the two food sources, we can determine the percentage of the material mixed in the gut contents of *A. abyssorum* that is contributed by each of the end members with the following calculation:

Proportion of foregut material comprised of sediment trap material

$$= \frac{(FG - SS) \times 100}{(ST - SS)}$$

where *FG* is mean excess ^{210}Pb activity of foreguts, *SS* is mean excess ^{210}Pb activity of surface sediments, and *ST* is mean excess ^{210}Pb activity of sediment trap material. The calculation, using measured activities of excess ^{210}Pb in sediment trap samples, surface sediments (0–2.5 mm), and animal guts, shows that ~91% (range 56–100% using ± 1 SD) of gut content material must have come from sediment trap material rather than the bulk surface sediment (Table 1). Qualitative microscopic analysis of the foregut content of three *A. abyssorum* revealed very little background sedi-

ment; instead, the contents resembled the particles and phytoplankton remains found in detrital aggregates, confirming ingestion of predominantly newly settled material (S. Beaulieu in prep.). This observation suggests that mobile megafauna utilize newly settled particulate matter and documents the potential for selective feeding on the freshest particles. Whether the mechanism for selective ingestion is location and uptake of discrete aggregate patches or simply discrimination between surficial sediments and freshly deposited particles, or a combination of both, is unknown; regardless of the method, ingestion of the bulk surface sediment itself seems to be minimal.

Excess ^{234}Th activity and $^{234}\text{Th} : ^{210}\text{Pb}$ activity ratios of sediment trap material, detrital aggregates, and animal gut contents all were clustered together at high values, in contrast to surface sediments from which they were much lower (Fig. 1). Excess ^{234}Th activities of sediment trap material ($n = 9$) were highest, with activities of detrital aggregates B ($n = 3$), *A. abyssorum* foreguts ($n = 5$) and hindguts ($n = 9$), and *O. mutabilis* fore- and hindgut ($n = 1$ each) clustering just below these values. Excess ^{234}Th activities of two detrital aggregate samples (A) were lower than in the other samples (Fig. 1). The lower values could reflect real differences in

composition and age or could be an artifact of sample processing (the extremely high salt content of these two samples could have precluded an accurate salt correction to measured mass). However, ^{234}Th activities of these two samples were still 7–8 times greater than the highest surface sediment samples ($n = 11$). Excess ^{234}Th activities of surface sediments (0–5 mm) were all below 37 disintegrations per minute per gram dry weight [$\text{dpm} (\text{gDW})^{-1}$], <3% of the activities of sediment trap samples and most of the gut content samples (Fig. 1).

Mean apparent ages also illustrate how different bulk sediments were from sediment trap, aggregate, and gut content samples (Table 1). Mean apparent ages were calculated with the equation

$$\text{Age} = -\left(\frac{1}{\lambda}\right) \times \ln \left[\frac{\left(\frac{^{234}\text{Th}_{\text{excess}}}{^{210}\text{Pb}_{\text{excess}}}\right)_{t=x}}{\left(\frac{^{234}\text{Th}_{\text{excess}}}{^{210}\text{Pb}_{\text{excess}}}\right)_{t=0}} \right],$$

where λ is the decay constant of ^{234}Th , and the assumption that any change in the ratio was due to decay of excess ^{234}Th . Based on the results of the previous calculation (91% of the gut content = sediment trap material), we assumed for this calculation that all of the material in the guts was sediment trap material (i.e. the material in the gut initially had the same $^{234}\text{Th} : ^{210}\text{Pb}$ ratio as the sediment trap material). Setting the age of sediment trap material at zero resulted in aggregate apparent ages of 20 d (group A) and <0 d (group B). The very young mean apparent age of the group B aggregates indicates that this material was as fresh as the sediment trap material and was not sitting on the sea floor for very long before collection. Mean foregut and hindgut ages were ~13 and ~12 d, respectively, whereas surface sediment ages were >100 d.

The mean statistical counting error (Friedlander et al. 1981) for ^{234}Th and ^{210}Pb activities of fore- and hindguts was $7.1 \pm 3.6\%$ ($n = 28$, range 1.8–16.2%). These errors preclude detection of an age change between fore- and hindgut material of <6 d. We did not observe a change ≥ 6 d and therefore conclude that most of the ingested material passes through the gut in less than 6 d.

The role of mobile epibenthic megafauna in the fate of settling particulate matter can be demonstrated in part by calculating the proportion of the vertical mass flux that could potentially be processed by a given population of animals. Using the range of densities of *A. abyssorum* from nine towed camera-sled transects (1.6–3.8 ind. 100 m^{-2} ; Lauerman et al. 1996), a gut passage time of 6 d, and the range of gut content masses (0.17–1.3 g), we calculated the range of grams of sediment that could be ingested $\text{m}^{-2} \text{ d}^{-1}$. Comparing these values to the mean downward mass flux (0.19 $\text{g m}^{-2} \text{ d}^{-1}$; from sediment trap samples), we calculated that this population of holothuroids could potentially process 0.2–4% of the vertical flux ($\text{m}^{-2} \text{ d}^{-1}$) during the high flux period of the year, assuming 91% of the gut mass was fresh material. If residence time in the gut is <6 d, the percentage

of vertical flux processed is even greater. The spatial variability in animal density, indicated by the range found among nine transects, means that the processing of settling particles by *A. abyssorum* also will be spatially heterogeneous.

The percentage of vertical flux ingested and processed by the entire assemblage of mobile epibenthic megafauna could be substantially greater than that calculated for *A. abyssorum* alone. The holothuroids *Elpidia minutissima*, *Peniagone vitrea*, and *Peniagone diaphana* are commonly observed, and *Scotoplanes globosa*, *O. mutabilis*, *Psychropotes longicauda*, and *Synallactes profundus* are present as well, though less abundant. Two echinoids, *Echinocrepis* sp. and a regular urchin, also are common. Combined, densities of these taxa ranged from 30 to 65 individuals 100 m^{-2} and these values increase to 90–140 individuals 100 m^{-2} when the four common ophiuroid species are included (Lauerman et al. 1996). We clearly have documented utilization of ^{234}Th -rich fresh particulate material by *A. abyssorum*. The high excess ^{234}Th activity found in the gut of the one specimen of *O. mutabilis* analyzed suggests that this species also may selectively ingest freshly deposited material. If even a few of the other species are trophically similar, the proportion of the vertical flux of particles processed collectively by the assemblage of mobile megafauna would be substantially greater than the 4% calculated for a single species.

The mobility of these epibenthic species also will affect the distribution of recently settled particles (K. L. Smith et al. 1993; Wheatcroft 1991). Mobile megafauna can serve as concentrating agents, repackaging ingested matter while moving laterally across the sediment surface and then depositing the reworked material in a new location in the form of fecal casts. For a given square meter of sea floor, an animal emigrating may clear a large swath of recently settled particles as it moves laterally across the bottom. Another animal, immigrating into this square meter, may redeposit a quantity of fresh particles equivalent to that consumed by the other animal but in the form of a fecal cast.

During movement through the animal's gut prior to defecation, the ingested particles may be altered. Sibuet et al. (1982) examined modification of the gut contents in the digestive tract of two species of abyssal holothuroids in the North Atlantic. They report changes in concentrations of bacteria, water-soluble and alkali-soluble proteins and carbohydrates, and refractory nitrogen, as well as absorption efficiency, between successive segments of the guts. Degradation of photosynthetic pigments from one end of the gut to the other can also occur in deep-sea holothuroid guts (Billett et al. 1988). Pfannkuche and Lochte (1993) traced cyanobacteria from sedimenting salp fecal pellets into the guts of two species of North Atlantic deep-sea holothuroids and their fecal casts and concluded that cyanobacteria may not be readily digested. Thus, the chemistry of the redeposited material and the area of sea floor that it covers will not be equivalent to that removed by the feeding animal. Therefore, by their movement, epibenthic megafauna can alter the availability of fresh particles to infaunal organisms and also the form in which particles are available (untouched homogeneous layer vs. well mixed into sediment vs. fecal cast). Based on analysis of time-lapse photographs, the mobile epi-

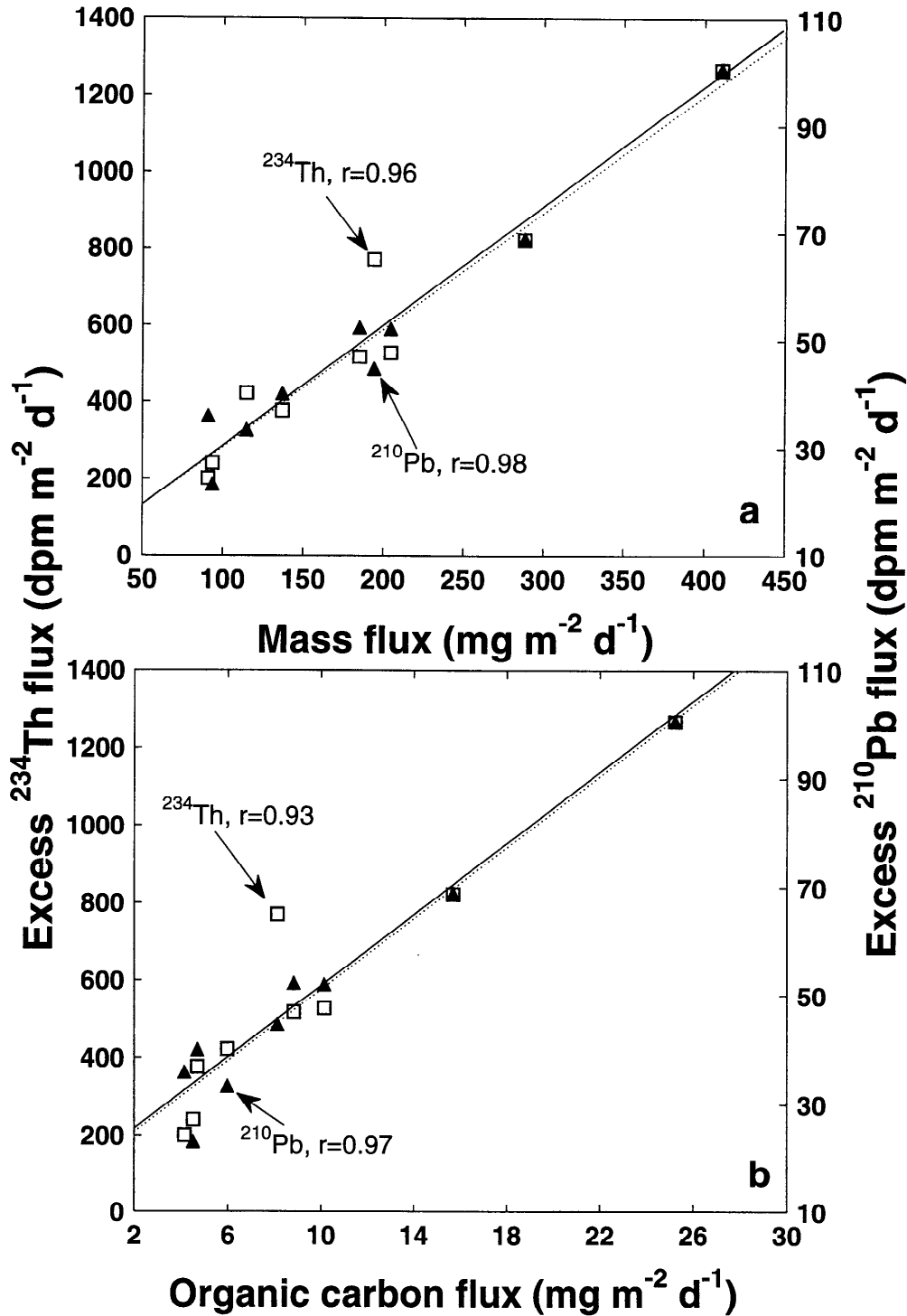


Fig. 2. Relationships between (a) mass flux and excess ^{234}Th and excess ^{210}Pb fluxes and (b) organic carbon flux and excess ^{234}Th and excess ^{210}Pb fluxes. Lines represent a linear fit to the data points.

benthic echinoderm assemblage was estimated to transit at least 88% of a 20-m² area over a 3-month period at Sta. M (K. L. Smith et al. 1993). Assuming these animals ingest a large proportion of the freshly settled material in their paths, they are relocating substantial quantities of material, effectively horizontally reorganizing the recent sedimentary record.

The ingestion and horizontal movement of recently settled particles by megafauna has important implications for the study of diagenetic reactions, and potentially, carbon degradation. In the open ocean, excess ^{234}Th and ^{210}Pb fluxes are positively correlated with variations in both mass particle flux and organic carbon flux and have been suggested as proxies for organic carbon delivery to the benthos (Moore

and Dymond 1988; Thunell et al. 1994). For our sediment traps samples, both excess ^{234}Th and ^{210}Pb fluxes were positively correlated with mass and organic carbon fluxes (Fig. 2). Percent carbon values were higher in the sediment trap samples (4.75 ± 0.76 , $n = 13$; Baldwin et al. in prep.) and aggregates (5.21 ± 2.07 , $n = 145$; Baldwin et al. in prep) than in the surface sediment samples (1.76 ± 0.03 , $n = 4$; in the range reported in Smith et al. 1994). Excess ^{234}Th and ^{210}Pb followed the same trend, suggesting that animals are ingesting material rich in organic carbon. If ^{234}Th proves to be a robust proxy for organic carbon, ingestion of freshly settled material could be converted to organic carbon uptake and used in carbon budget calculations.

We have found that freshly settled particles can comprise a large proportion of mobile epibenthic megafaunal gut contents, at least during high flux periods, and conclude that the contribution of this mainly deposit-feeding group to nutrient cycling and sedimentation processes in the deep sea needs to be considered. The effects of large deposit-feeding animals, such as echiuran worms in the Santa Catalina Basin, on vertical mixing of sediments has received attention (Smith et al. 1986), but the trophic link between settling particles and abyssal mobile epibenthic megafauna has not been addressed in many studies of biological effects on sediment processes. However, selective feeding by deep-sea deposit feeders in general has been suggested in models of age-dependent (C. R. Smith et al. 1993) and size-dependent (Wheatcroft 1992) mixing of particles. Based on the theory of age-dependent mixing, C. R. Smith et al. (1993) predicted that gut contents of deep-sea deposit feeders should have high activities of radionuclides with short half-lives. Smith et al. (1996) found ^{234}Th - and ^{210}Pb -rich phytodetrital material on the sediment surface and in animal burrows at depths of 17–27 cm in the equatorial Pacific, suggesting rapid use of fresh material by megafauna living in the sediments. Our finding of selective ingestion of ^{234}Th -rich particles by mobile epibenthic megafauna also confirms the prediction of age-dependent mixing. The mobility of many of these species adds the potential for horizontally redistributing recently settled material over the sediment surface (Wheatcroft 1991; K. L. Smith et al. 1993) and for changing the chemistry of these particles in the process. By concentrating recently settled particles into fecal casts these animals increase horizontal heterogeneity, making one-dimensional bioturbation models that assume horizontal homogeneity more problematic. A strong horizontal transport and mixing component mediated by mobile epibenthic megafauna should be considered in addition to the vertical component attributed to infauna in sediment-mixing models.

Echinoderms are a major component of many deep-sea epibenthic communities, contributing significantly to deep-sea benthic biomass (Sibuet and Segonzac 1985) and energy reserves (Walker et al. 1987a,b). Seasonal peaks in the deposition of detrital matter to the deep sea, reported from the North Atlantic (Billett et al. 1983; Lampitt 1985), North Pacific (K. L. Smith et al. 1993, 1994), and equatorial Pacific (Smith et al. 1996), also seem to be widespread. The rapid ingestion of ^{234}Th -rich, freshly settled particles by mobile epibenthic megafauna and the potential for significant horizontal effects on sediment processes mediated by their mo-

bility, observed during a high flux period at Sta. M, may be relevant in other parts of the ocean as well.

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Acknowledgments

We thank the crew of the RV *New Horizon*, RV *Atlantis II*, and the *Alvin* group for invaluable help while at sea. We also thank R. Baldwin, S. Beaulieu, J. Drazen, J. Gieskes, R. Hessler, N. Holland, R. Kaufmann, J. Krest, and L. Levin for critical reviews of the manuscript and R. Baldwin for help with initial sample processing. Two anonymous reviewers gave helpful suggestions for improving this manuscript.

This work was supported by NSF grants OCE 89-22620 and OCE 92-17334 (K.L.S.) and a Sigma Xi grant (L.M.L.L.).

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Submitted: 15 April 1996

Accepted: 9 September 1996

Amended: 8 December 1996

Estimation of f -ratios in oceans based on phytoplankton size structure

Abstract—Several equations to estimate the vertical export of particulate organic carbon from the ocean's euphotic zone (POC_E) use variables that are determined at sea or are derived from remote sensing. One of the approaches requires reliable estimates of f -ratios (NO_3^- uptake/total N uptake) that can be either determined directly from N uptake by phytoplankton or derived from total phytoplankton Chl a biomass or production (P_T) or from NO_3^- concentrations. By using a combination of theoretical considerations and field measurements, we show that f -ratios are linear functions of size-fractionated ($>5 \mu\text{m}$ /total) phytoplankton production (P_L/P_T) and biomass. Comparison of our model with the more usual f -ratio = $f(P_T)$ shows that the large residuals are spread over the range of P_L/P_T in the former, whereas they are concentrated at low P_T in the latter. Because P_T is low in most of the world oceans most of

the time, use of our model may significantly improve the estimates of f -ratio and thus of POC_E .

Because the oceans may be an important sink for the rapidly increasing concentration of anthropogenic CO_2 , a central objective of major biological oceanographic programs is to quantify, model, and predict, at global and annual scales, the flux of biogenic carbon to deep waters. There are several published equations that estimate the vertical export of particulate organic carbon from the ocean's euphotic zone (POC_E) with variables that are determined at sea or derived from remote sensing of ocean color and sea surface temperature.