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Evaluation of excess ^{234}Th activity in sediments as an indicator of food quality for deep-sea deposit feeders

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ABSTRACT

Deep-sea deposit feeders selectively ingest large volumes of sediment. Knowledge of the nature of this selectivity will help to elucidate the limiting nutritional requirements and geochemical impacts of these abundant animals. Shallow-water and theoretical studies suggest that deep-sea deposit feeders should select particles rich in protein, bacterial biomass, and/or chloropigment concentrations. Recent studies indicate that deep-sea megafaunal deposit feeders exhibit strong gut enrichment of excess (xs) ^{234}Th activity, even though $^{234}Th_{xs}$ lacks nutritional value. To explore the significance of selective ingestion of $^{234}Th_{xs}$ activity, we evaluated the correlations between $^{234}Th_{xs}$ activity and three potential tracers of deposit feeder food quality: chlorophyll *a* (chl *a*), enzymatically hydrolyzable amino acids (EHAA), and adenosine triphosphate (ATP). Surface sediments from three quiescent bathyal basins off Southern California (San Nicolas, Santa Catalina, and San Clemente) were collected by a multiple corer and analyzed for $^{234}Th_{xs}$ activity, chl *a,* EHAA, ATP, and total organic carbon and nitrogen. $^{234}Th_{xs}$ activity was positively correlated with chl *a* and phaeopigment concentrations and negatively correlated with EHAA concentrations. Excess ^{234}Th was not linearly correlated with concentrations of ATP, organic carbon, or total nitrogen. The results suggest that deep-sea deposit feeders select sediments with high $^{234}Th_{xs}$ activity because it is associated with recently settled phytodetrital material. There is no evidence that this $^{234}Th_{xs}$-rich material has particularly high concentrations of labile amino acids or microbial biomass. Phytodetrital material may be an important source of some other limiting nutrient to deep-sea deposit feeders, e.g., polyunsaturated fatty acids, labile organic carbon and/or vitamins.

1. Introduction

Deposit-feeding megafauna occur throughout the deep sea and influence seafloor cycling of organic matter through the ingestion, digestive alteration, and egestion of sediment particles (e.g., Gage and Tyler, 1991; Miller *et al.,* 2000). Megafaunal deposit feeders can traverse and feed on large portions of the seafloor over time scales of days to

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months, in the process altering the microbial and chemical composition of the sediments (e.g., LaFond, 1967; Plante and Jumars, 1992; C. Smith, 1992; K. Smith *et al.,* 1993; A. Smith *et al.,* 1997; Miller *et al.,* 2000).

Despite consuming sediments at high rates, shallow-water species are known to feed very selectively on particles characterized by small size, low specific gravity, and organic coatings. This selectivity is postulated to increase the uptake of microbial biomass and/or labile organic material (Lopez and Levinton, 1987; Wheatcroft, 1992; C. Smith *et al.,* 1993). The feeding rates and selectivity of deep-sea deposit feeders are poorly understood compared to shallow-water counterparts. However, in food-limited environments, optimal foraging theory suggests that deep-sea deposit feeders should be highly selective for limiting nutritional components (e.g., Taghon and Jumars, 1984; Taghon and Greene, 1990). A limited number of studies indicate that deep-sea deposit feeders do feed very selectively because proteins, lipids, carbohydrates, and chloropigments can be heavily enriched in gut sediments compared to surrounding sediments (Khripounoff and Sibuet, 1980; Sibuet, 1988; Billet *et al.,* 1988; Thiel *et al.,* 1988/1989; Pfannkuche and Lochte, 1993; Miller *et al.,* 2000). In addition, gut sediments of surface deposit feeders from a number of quiescent deep-sea habitats are extremely enriched in $^{234}Th_{xs}$ activity, a particle-reactive radioisotope that has a short half-life (24.1 d). Excess ^{234}Th activity in the gut sediments of deep-sea deposit feeders often is orders of magnitude greater than surrounding sediments (Lauerman *et al.,* 1997; Miller *et al.,* 2000; Smith *et al.,* 2001), with values commonly comparable to those activities in associated particle trap samples. The high excess ^{234}Th activities in guts do not appear to result from gut concentration processes (Shull and Mayer, 2002), but rather from selective ingestion. Clearly, deposit feeders are not selecting sediment particles specifically for ^{234}Th content because ^{234}Th itself has no nutritive value. Consequently, $^{234}Th_{xs}$ activity appears likely to co-vary with some specific food quality of the sediment. Knowledge of the relationship between $^{234}Th_{xs}$ activity and various measures of food quality should provide insights into the feeding selectivity (and potential limiting nutritional requirements) of deep-sea deposit feeders. It may also allow $^{234}Th_{xs}$ activity to be used as a proxy for specific aspects of deposit-feeder food quality.

Key parameters used in previous studies to estimate sediment food quality for deposit feeders include photosynthetic pigments, enzymatically hydrolyzable amino acids (EHAA), adenosine triphosphate (ATP), and total organic carbon and nitrogen. Chlorophyll *a* (chl *a*) and phaeopigments are labile compounds found in fresh phytoplankton and are used as indicators of recently deposited phytodetritus (Thiel *et al.,* 1988/1989; Sun *et al.,* 1991; C. Smith *et al.,* 1996; Stephens *et al.,* 1997). Several studies have suggested that deep-sea and shallow-water deposit feeders may be organic-nitrogen limited (Jumars *et al.,* 1990; Mayer *et al.,* 1995). Measurements of EHAA yield an estimation of the bioavailable pool of amino acids, which are potentially a major source of organic nitrogen to deep-sea deposit feeders (Mayer *et*

al., 1995). ATP is a measure of "microbial" (including bacterial, archaeal, protozoan and meiofaunal) biomass (Karl and Craven, 1980), which may meet some of the organic carbon and nitrogen requirements of deposit feeders (Lopez and Levinton, 1987). Finally, total organic carbon and nitrogen may provide rough indications of food availability to deposit feeders (e.g., Levin *et al.,* 1994).

Thorium-234 is a particle-reactive radioisotope produced in the water column by its soluble parent, ^{238}U. Because ^{234}Th is highly insoluble, it is scavenged from the water column by sinking particles. Due to its short half-life, the deficit of this isotope in the euphotic zone can be used as a tracer for estimating rates of particulate organic carbon (POC) export (Bacon and Anderson, 1982; Buesseler *et al.,* 1992; Buesseler, 1998). A small fraction of this new production reaches the sea floor in the form of flocculent material, phytodetritus, and fecal pellets, where it may be consumed by the deep-sea benthos (e.g., Iseki, 1981; Alldredge and Silver, 1988; Riemann, 1989; Hecker, 1990; Gage and Tyler, 1991; C. Smith *et al.,* 1996). New particles sinking from the surface ocean are enriched in ^{234}Th due to thorium scavenging. This enrichment is called "excess activity" because it exceeds the ^{234}Th activity supported by the decay of ^{238}U within the particles. Over a time scale of ~100 days after a particle reaches the seafloor, the excess ^{234}Th activity decays away (Aller and DeMaster, 1984). Accompanying this loss, labile organic matter associated with particles from the euphotic zone also degrades, presumably lowering the food value of the particles. Given the nature of ^{234}Th scavenging in the upper ocean, $^{234}Th_{xs}$ activity and labile organic material most likely arrive at the deep-sea floor on similar particles, and this labile organic fraction is the ultimate energy source for deposit feeders (C. Smith *et al.,* 1993; Lauerman *et al.,* 1997). If $^{234}Th_{xs}$ activity and the labile organic fraction are indeed associated with similar particles, it is possible that $^{234}Th_{xs}$ activities are correlated with measurements of food quality, e.g., chl *a,* phaeopigments, EHAA, ATP, and organic carbon and nitrogen.

In this study, we examined the relationship between $^{234}Th_{xs}$ activity and a variety of parameters related to food quality in deep-sea sediments to gain insights into the feeding selectivity and nutrition of deep-sea deposit feeders. Deposit feeders in all three basins studied (Santa Catalina, San Nicolas, and San Clemente) exhibited strong gut enrichment of $^{234}Th_{xs}$ activity (Fornes, 1999; Miller *et al.,* 2000; C. Smith *et al.,* 2001). Data were collected in quiescent bathyal basins specifically to determine whether excess ^{234}Th activity in surface sediments is positively correlated with chl *a,* phaeopigments, ATP, EHAA, organic carbon or total nitrogen concentrations in low-energy, deep-sea habitats.

Because the gut contents of surface deposit feeders are known to be especially enriched in $^{234}Th_{xs}$ activity (Fornes, 1999; Miller *et al.,* 2000), we explored the relationship between $^{234}Th_{xs}$ activity and food quality in the surficial layer of sediments (the top 5 mm), i.e., within the putative feeding zone of surface deposit feeders. In addition, we explored the correlation between $^{234}Th_{xs}$ activity and food-quality concentrations as a function of depth

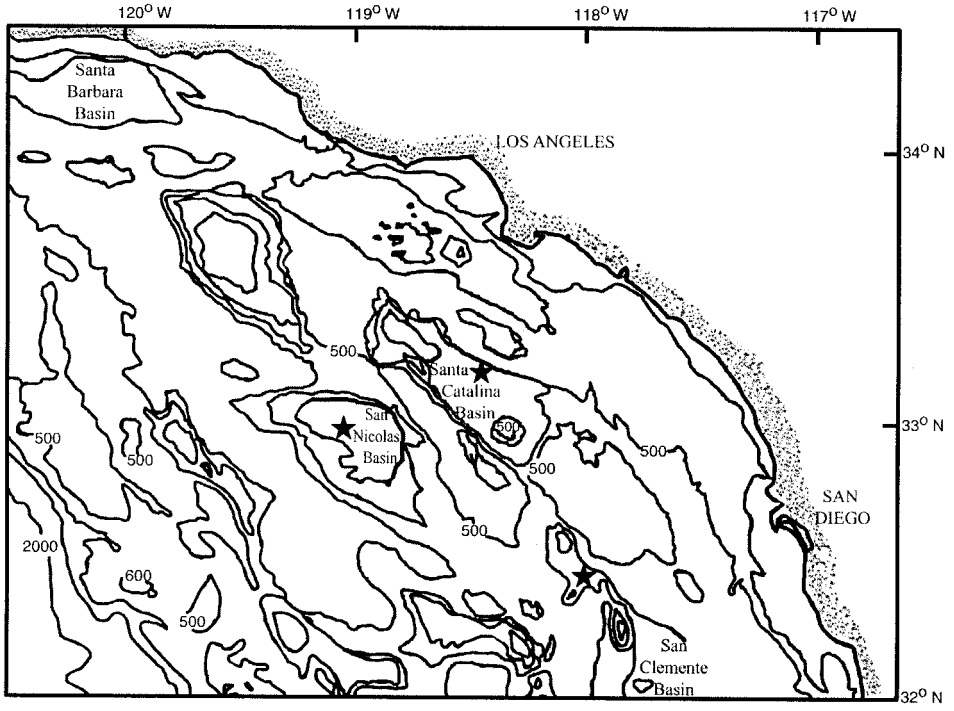

Figure 1. Location of study areas at the Santa Catalina, San Nicolas, and San Clemente basins (stars). Depth contours in fathoms. (Modified from Eppley, 1986).

in the sediment because subsurface deposit feeders can also exhibit gut enrichment of $^{234}Th_{xs}$ activity (Miller *et al.,* 2000; C. Smith *et al.,* 2001).

2. Study sites

Three quiescent basins in the California Borderland were sampled in April 1998: Santa Catalina, San Nicolas, and San Clemente. The basins range in depth from 1200 to 2000 m (Fig. 1). These low-energy, flat-bottomed basins are characterized by poorly sorted silt-clay sediment and sedimentation rates of ~12–21 cm per ky (Emery, 1960; Smith and Hamilton, 1983; Fornes, 1999). Bottom water O_2 concentrations range from 18 to 22 μM for Santa Catalina and San Nicolas basins, to 58 μM for San Clemente Basin (Emery, 1960; Archer *et al.,* 1989). Organic-carbon flux is relatively constant across the basins, ranging from 0.013 to 0.05 g C m^{-2} y^{-1} (Fornes *et al.,* 2001). Deep-sea animals from these basins are well described, and Santa Catalina Basin in particular has been the site of numerous studies of benthic ecology and carbon flux (e.g., Jumars, 1976; Fauchald and Jones, 1978; Smith and Hamilton, 1983; C. Smith, 1985, 1986; K. Smith *et al.,* 1987; Kukert and Smith, 1992; Smith and Demopoulos, 2003).

3. Methods

a. Field methods

Sediment cores were collected using a multiple corer (Gage and Tyler, 1991), which yielded cores (10 cm diameter, 80 cm^2 area) virtually undisturbed by bow-wave effects (Barnett *et al.,* 1984). Sediment cores were sectioned at 0.5 cm intervals down to 2 cm according to the methods of C. Smith *et al.* (1993), and the outer few millimeters were cut away at each depth interval to minimize contamination from vertical smearing. Equivalent levels from two core tubes were combined from each multicore lowering to provide sufficient sediment volume to conduct all desired analyses. The core tubes combined were separated by 20 to 40 cm. Each combined sediment sample was homogenized and subsampled for ATP, chl *a,* phaeopigment, EHAA, organic carbon and nitrogen, and ^{234}Th analyses. Samples for pigment measurements were frozen in liquid nitrogen and stored at −80°C. Samples for ATP, EHAA, organic carbon and total nitrogen were stored at −20°C.

b. Laboratory methods

Excess ^{234}Th activity was measured using a modified version of the methods described in Aller and DeMaster (1984) and Fornes *et al.* (2001). Thorium-234 activity was isolated and then measured on a low level, gas flow, anti-coincidence beta counter. Uranium-238 activities were measured by alpha spectroscopy. Thorium-234 activities were converted to excess values by subtracting ^{238}U activity from total ^{234}Th activity and correcting for decay since sample collection. All ^{234}Th activities discussed in this manuscript are excess activities expressed in dpm g^{-1} dry sediment (corrected for salt content).

ATP analyses followed the methods of Karl and Craven (1980). Fresh sediment samples were homogenized and extracted in 0.5 M H_3PO_4 for 10 min at 4°C. Three replicates from each 0.5 cm section were then centrifuged, and 500 μL of the supernatant was removed and pipetted into vials. To each vial, 1 mL of Tris buffer was added, and the samples were subsequently frozen at −80°C. From each sample, two subsamples were taken, and an internal ATP standard was added to estimate adsorptive and other losses of extracted ATP (Karl and Craven, 1980; Craven and Karl, 1984). The average percent recovery for the internal ATP standard was 75% (range 65–85%). In the laboratory, samples were thawed, and firefly lantern extract (Sigma FLE-50) was prepared in a mixture of $MgSO_4$ and arsenate buffer. ATP in the extracts was measured according to Karl and Craven (1980) and analyzed using the firefly luciferase-luciferin bioluminescence assay.

For pigment analyses, sections of frozen sediment (~1 g) were vortexed after thawing, sonicated in a dark ice bath for 10 minutes, and then extracted overnight at −20°C in the dark in 5 ml of 100% acetone in glass tubes (Sun *et al.,* 1991). Samples were then centrifuged at 3000 rpm for 5 min and the extract decanted. Each sample was extracted three times and the extracts were combined. Fluorescence of extracts was measured at a wavelength of 670 nm using a Turner model 10-AU fluorometer. Chl *a* and phaeopigment concentrations were calculated based on a pure chl *a* standard (Sigma Chemical Co.) and acidification. Values were normalized to salt-corrected dry weights of extracted sediment.

Concentrations of enzymatically hydrolyzable amino acids (EHAA) in sediments were analyzed using the methods of Mayer *et al.* (1995). A single measure of total amino acids was made by adding OPA reagent to the resultant hydrolysite and the fluorescence was measured on a Perkin-Elmer Model LS-5 Fluorescence Spectrophotometer at excitation/emission wavelengths of 340/452 nm.

Sedimentary organic carbon and total nitrogen were analyzed using the methods of Levin and Thomas (1989). Subsamples of sediment were dried for 24 hrs at 60°C, acidified with sulfurous acid, and weighed. The resulting sample was run on a Perkin-Elmer 2400 CHN analyzer along with a series of acetanilide reference standards. A standard curve was used to determine carbon and nitrogen concentrations, and C/N ratios of the samples.

In order to make comparisons across three basins and resolve between-basin variations, data within a basin were normalized by dividing each datum by the average basin concentration for that parameter. Each data point plotted represents concentrations from one multicore drop for each basin. For San Nicolas Basin, the $n = 4$ drops, for San Clemente Basin, $n = 2$ drops, and for Santa Catalina Basin, $n = 3$ drops. To examine relationships among variables, the product moment correlation and Spearman's ρ (rank correlation coefficient) were used (Sokal and Rohlf, 1969). For sediment profile comparisons, correlation coefficients were calculated for each profile, and the probabilities combined to obtain an overall level of significance (Sokal and Rohlf, 1969). A p-level of 0.05 was used as the criterion for statistical significance.

4. Results

Concentrations of chl *a,* phaeopigments, EHAA, ATP, total organic C, total N, C/N ratio and $^{234}Th_{xs}$ activity from each of the basins, including profile data from San Clemente Basin, are reported in Table 1. Excess ^{234}Th activity varied four fold within basins for the 0–0.5 cm layer, while EHAA, chl *a,* and phaeopigments varied by ≤50%. The deepest study site, San Clemente Basin, had the lowest chl *a* concentration and relatively low phaeopigment, organic carbon, and total nitrogen concentrations.

Excess ^{234}Th activity was plotted against chl *a,* phaeopigments, EHAA, ATP, organic carbon, and total nitrogen (Fig. 2). Excess ^{234}Th activity in surface sediments for all basins pooled was positively correlated (product moment correlation, $p < 0.005$) with chl *a* and phaeopigment concentrations. Chl *a* was positively correlated with phaeopigments ($r = 0.9396$, $p < 0.001$). There was a significant negative correlation between $^{234}Th_{xs}$ activity and concentrations of EHAA. However, no significant relationships were found between $^{234}Th_{xs}$ activity and concentrations of ATP, total nitrogen, or organic carbon. Finally, a significant negative correlation was found between chl *a* and EHAA concentration (Fig. 3), but no significant relationship was found between ATP and chl *a* concentration or EHAA and ATP concentration.

Sediment profiles (0–1.5 cm) from San Clemente Basin were examined for $^{234}Th_{xs}$ activity, and concentrations of chl *a,* phaeopigments, EHAA, ATP, organic carbon, and total nitrogen. Profiles of $^{234}Th_{xs}$ activity showed decreasing activity with depth in

Table 1. $^{234}Th_{xs}$ activities, concentrations of chlorophyll *a*, phaeopigments, EHAA, ATP, organic carbon, total nitrogen, and C/N ratios (weight:weight) in sediments collected in April 1998 from San Clemente, Santa Catalina, and San Nicolas basins. Data represent the mean values ± 1 standard error.

Location/Sample #	Section	$^{234}Th_{xs}$ (dpm/g)	Chl *a* (μg/g)	Phaeo (μg/g)	EHAA (mg/g)	ATP (μg/g)	Org. C (mg/g)	Org. N (mg/g)	C/N ratio (wt/wt)
San Clemente Basin									
CRS 355	0–0.5 cm	9.63 ± 0.83	9.86 ± 0.78	27.23 ± 1.18	0.49 ± 0.02	0.60 ± 0.02	29.73 ± 1.52	4.23 ± 0.15	7.01 ± 0.12
	0.5–1.0 cm	0 ± 0.3	6.49 ± 0.00	16.97 ± 0.12	0.57 ± 0.05	0.38 ± 0.02	31.11 ± 0.18	4.48 ± 0.02	6.95 ± 0.07
	1.0–1.5 cm	0 ± 0.4	6.50 ± 0.44	15.47 ± 0.16	0.35 ± 0.03	0.28 ± 0.03	29.68 ± 1.47	4.35 ± 0.21	6.81 ± 0.02
CRS 360	0–0.5 cm	23.60 ± 1.7	10.24 ± 0.23	32.13 ± 1.06	0.52 ± 0.00	1.64 ± 0.02	31.28 ± 0.31	3.89 ± 0.03	8.03 ± 0.20
	0.5–1.0 cm	0.6 ± 0.3	6.28 ± 0.04	18.56 ± 1.72	0.48 ± 0.01	3.25 ± 0.08	30.57 ± 1.52	3.80 ± 0.19	8.04 ± 0.01
	1.0–1.5 cm	0 ± 0.3	6.19 ± 0.09	16.17 ± 0.68	0.41 ± 0.03	3.97 ± 0.12	32.72 ± 0.60	3.93 ± 0.10	8.32 ± 0.05
Mean ± S.E.	0–0.5 cm	16.61 ± 6.98	10.05 ± 0.19	29.68 ± 1.12	0.51 ± 0.02	1.12 ± 0.52	30.51 ± 0.92	4.06 ± 0.09	7.52 ± 0.51
Santa Catalina Basin									
CRS 374	0–0.5 cm	7.90 ± 1.4	21.21 ± 0.71	43.18 ± 1.45	0.36 ± 0.01	0.95 ± 0.00	42.26 ± 3.06	5.34 ± 0.36	7.90 ± 0.04
CRS 375	0–0.5 cm	14.60 ± 1.5	25.27 ± 0.56	52.42 ± 1.54	0.21 ± 0.06	0.67 ± 0.03	46.77 ± 0.23	5.45 ± 0.05	8.58 ± 0.12
CRS 377	0–0.5 cm	7.38 ± 1.6	19.12 ± 0.16	38.22 ± 2.19	0.45 ± 0.03	1.38 ± 0.02	48.54 ± 0.81	5.48 ± 0.04	8.85 ± 0.08
Mean ± S.E.	0–0.5 cm	9.96 ± 2.33	21.57 ± 1.80	44.61 ± 1.73	0.34 ± 0.07	1.00 ± 0.20	45.85 ± 1.36	5.42 ± 0.15	8.44 ± 0.28
San Nicolas Basin									
CRS 379	0–0.5 cm	5.70 ± 1.5	15.31 ± 3.81	35.37 ± 8.19	0.58 ± 0.02	0.32 ± 0.01	50.97 ± 0.76	5.90 ± 0.14	8.63 ± 0.07
CRS 380	0–0.5 cm	10.19 ± 2.89	16.90 ± 0.79	38.38 ± 3.79	0.46 ± 0.08	0.54 ± 0.01	53.24 ± 0.54	6.47 ± 0.15	8.23 ± 0.27
CRS 382	0–0.5 cm	15.82 ± 5.22	21.85 ± 1.12	55.47 ± 1.60	0.38 ± 0.03	2.03 ± 0.02	50.83 ± 1.11	6.04 ± 0.22	8.42 ± 0.12
CRS 385	0–0.5 cm	22.49 ± 3.1	21.64 ± 0.92	61.22 ± 0.04	0.37 ± 0.02	0.26 ± 0.00	51.92 ± 0.99	6.10 ± 0.11	8.55 ± 0.00
Mean ± S.E.	0–0.5 cm	13.55 ± 3.63	18.74 ± 1.64	47.61 ± 3.40	0.45 ± 0.04	0.79 ± 0.42	51.74 ± 0.85	6.13 ± 0.15	8.46 ± 0.09

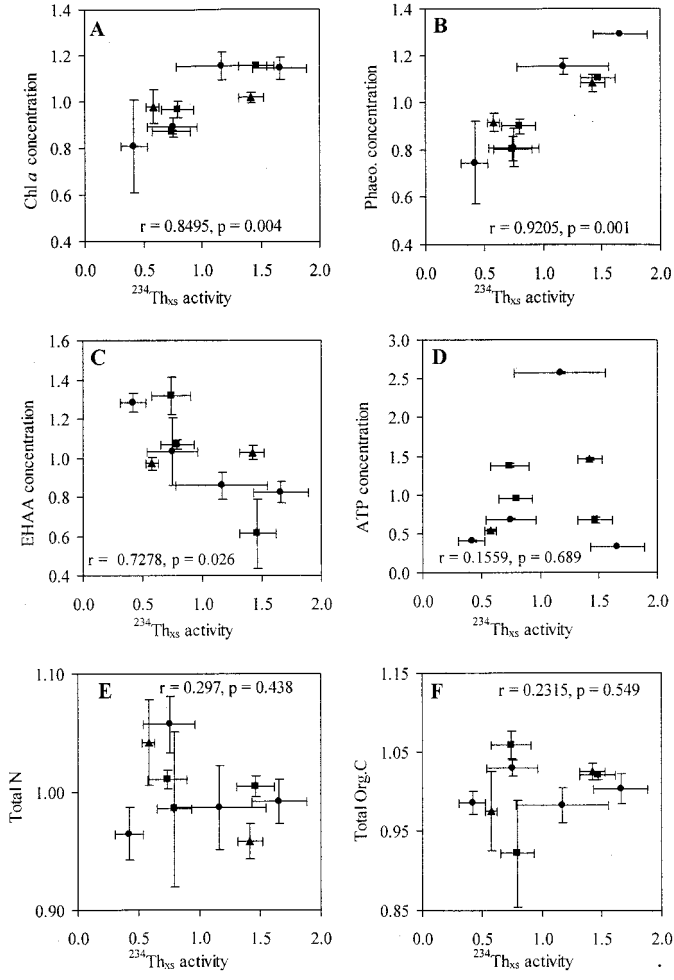

Figure 2. (A) chlorophyll *a,* (B) phaeopigments, (C) EHAA, (D) ATP, (E) total N and (F) organic C concentrations versus $^{234}Th_{xs}$ activity from the top 5 mm of sediment. Each point represents one multicore sample. Circles represent data from San Nicolas Basin, triangles from San Clemente Basin, and squares from Santa Catalina Basin. Data are normalized by dividing the values by the average values for that basin, e.g., [chlorophyll *a*]/mean [chlorophyll *a*] for that basin. Error bars represent one standard error based on three subsamples.

sediment (Fig. 4), such that no activity was present deeper than 0.5 cm depth. Sediment chl *a* concentration followed a similar pattern, with chl *a* decreasing with depth in the sediment (Fig. 4). Sediment phaeopigment concentration also decreased with increasing depth in the sediment (Fig. 4). When p-levels from both profiles were combined, $^{234}Th_{xs}$ activity was significantly positively correlated with chl *a* and phaeopigment concentrations (Fig. 5).

In contrast to $^{234}Th_{xs}$ activity and chl *a,* profiles of EHAA did not all decrease monotonically

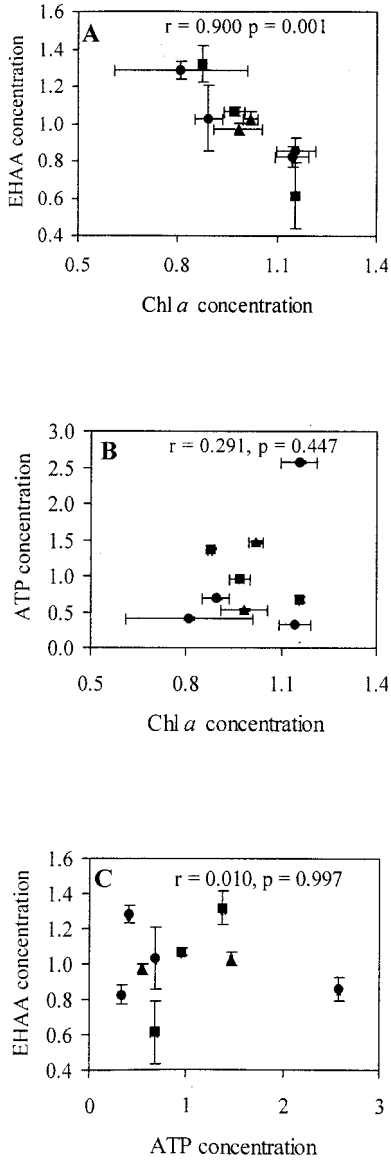

Figure 3. (A) EHAA and (B) ATP concentrations versus chlorophyll *a* concentration. (C) EHAA concentration versus ATP concentration. Error bars represent one standard error for two replicate subsamples. Circles represent data from San Nicolas Basin, triangles from San Clemente Basin, and squares from Santa Catalina Basin. Data are normalized by dividing the values by the average values for that basin, e.g., [EHAA]/mean [EHAA] for that basin. Error bars represent one standard error based on three subsamples. Standard errors for ATP concentrations were smaller than the symbol used in the figure.

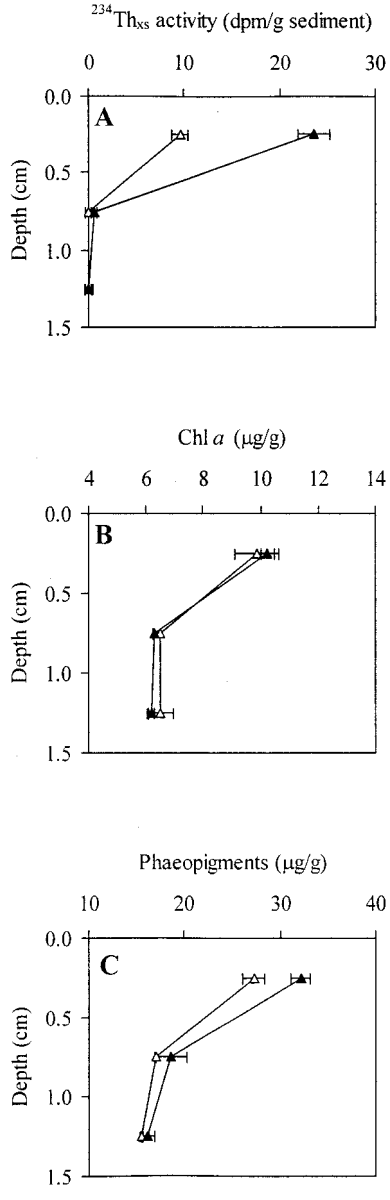

Figure 4. Sediment profiles of (A) $^{234}Th_{xs}$ activity, (B) chlorophyll *a* and (C) phaeopigment concentrations from two cores from San Clemente Basin. Horizontal error bars represent one standard error of two replicate samples. Open and closed triangles represent profile data from two separate multiple core drops.

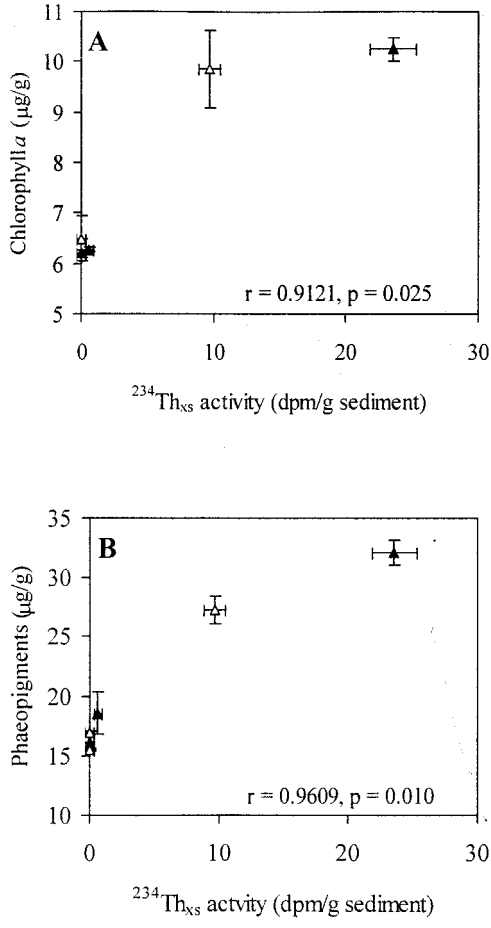

Figure 5. (A) chlorophyll *a* and (B) phaeopigment concentrations versus $^{234}Th_{xs}$ activity from 0–1.5 cm sediment from San Clemente Basin. Error bars represent one standard error for two replicate subsamples. Open and closed triangles represent profile data from two separate multiple core drops.

with sediment depth (Fig. 6). ATP concentration remained constant or increased with sediment depth (Fig. 6). Lastly, organic C and total N concentrations also remained relatively constant in the top 1.5 cm of sediment (Fig. 6). $^{234}Th_{xs}$ activities were not significantly correlated with concentrations of EHAA, ATP, organic carbon, or total nitrogen.

5. Discussion

The positive correlation between $^{234}Th_{xs}$ and chl *a* and phaeopigments in surface sediments and in sediment profiles is consistent with the idea that freshly deposited, chl *a*-rich sediments are also enriched in $^{234}Th_{xs}$ activity. This result is not unexpected because

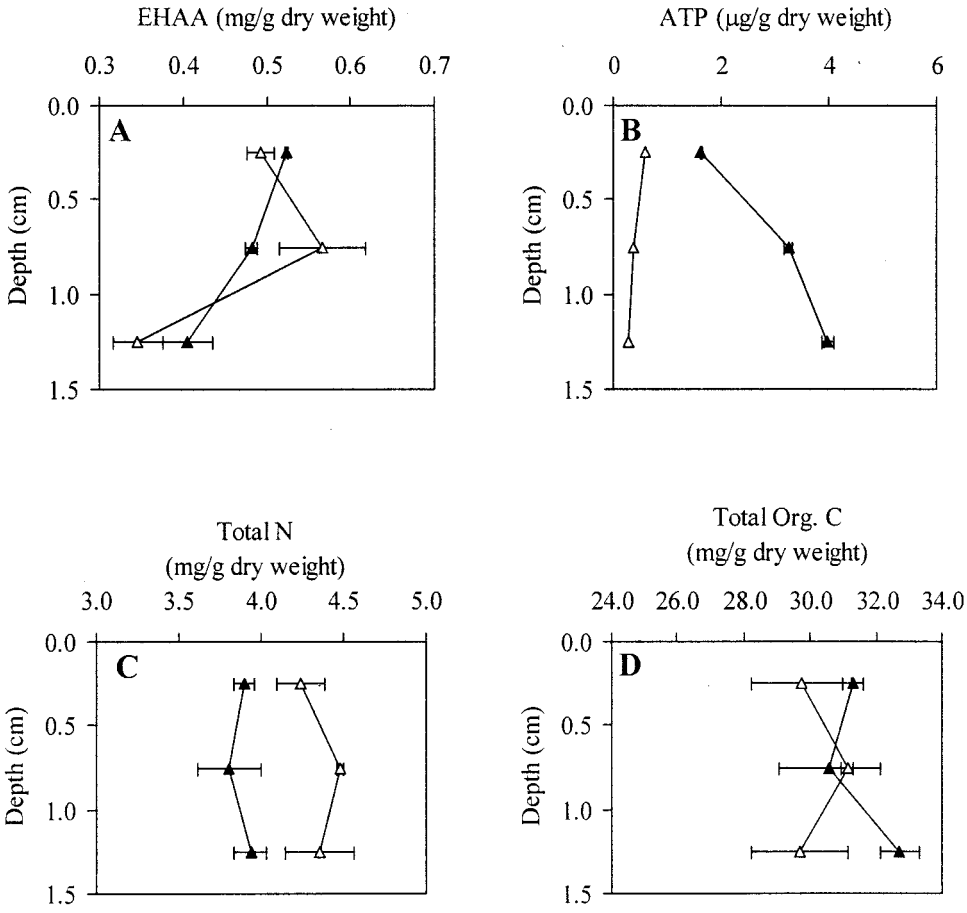

Figure 6. Sediment profiles of (A) EHAA, (B) ATP, (C) total nitrogen and (D) organic carbon concentrations from two cores from San Clemente Basin. Horizontal errors are one standard error of two replicate samples. Standard errors for ATP concentrations were smaller than the symbol used in the figure. Open and closed triangles represent profile data from two separate multiple core drops.

phytodetritus and $^{234}Th_{xs}$ activity are estimated to degrade on similar time scales (e.g., Lochte and Turley, 1988; C. Smith *et al.,* 1993; Stephens *et al.,* 1997), and phytodetritus has been shown to be rich in $^{234}Th_{xs}$ activity (Pope *et al.,* 1996; C. Smith *et al.,* 1996). Sediment chl *a* and phaeopigment concentrations from this study were comparable to those from sediments in other deep-sea habitats (Levin *et al.,* 1991; K. Smith *et al.,* 1994, 1998; Drazen *et al.,* 1998).

The negative correlation between $^{234}Th_{xs}$ activity and EHAA indicates that $^{234}Th_{xs}$ activity is not a reliable proxy for enzymatically available amino acids in the basin sediments on the scales studied. This result suggests that EHAA have slower turnover

times and/or different input functions than ^{234}Th, allowing relatively high amino acid concentrations to occur in sediment particles long after $^{234}Th_{xs}$ activity has decayed away. Sediment EHAA concentrations from this study were comparable to those from sediment studies in shallow-water and deep-sea habitats (Mayer *et al.,* 1995; Dell'Anno *et al.,* 2000). Potential sources of labile amino acids in the deep sea include phytodetritus and sediment microbes. However, EHAA concentrations were not positively correlated either with chl *a* or ATP concentrations. Therefore, the source of EHAA may be a combination of phytodetritus and microbial biomass.

The absence of a correlation between $^{234}Th_{xs}$ activity and ATP implies that $^{234}Th_{xs}$ activity is not a reliable indicator of microbial (including bacterial, archaeal, protozoan, and meiofaunal) biomass in surface sediments. In addition, in our study, ATP concentrations did not decrease within the top 1.5 cm of San Clemente Basin sediment, indicating that microbial biomass has different production and/or degradation functions than $^{234}Th_{xs}$ activity. The source of ATP is most likely deep-sea sediment microbes rather than microbes arriving on sinking particles, because sinking detritus appears to be a poor site for microbial growth (Karl *et al.,* 1988; Lochte and Turley, 1988; Turley and Lochte, 1990). Although microbes in deep-sea sediments have exhibited biomass increases following pulses of phytodetritus (Lochte and Turley, 1988; Turley and Lochte, 1990), we found no correlation between ATP-biomass and chl *a* concentration. We conclude that ATP-biomass may ultimately be controlled by phytodetrital input, but with growth-decline dynamics that differ from the exponential decay of $^{234}Th_{xs}$ activity.

The lack of correlation between $^{234}Th_{xs}$ activity and organic carbon or total nitrogen is very likely due to disparate turnover times. In contrast to $^{234}Th_{xs}$ activity, profiles of organic carbon and total nitrogen remained unchanged with increasing sediment depth, suggesting that turnover times for total organic carbon and nitrogen exceed the turnover times for $^{234}Th_{xs}$ activity. Because much of the organic matter in marine sediments is refractory, total organic carbon and nitrogen appear to be poor proxies for food value to deposit feeders (Lopez and Levinton, 1987).

The finding that $^{234}Th_{xs}$ activity is positively correlated with chl *a* and phytodetritus has important implications for deep-sea deposit feeders. Abyssal deposit feeders have been shown to selectively ingest recently deposited, chl *a*-rich phytodetritus (Billet *et al.,* 1988; Thiel *et al.,* 1988/1989; Moore and Roberts, 1994; Roberts *et al.,* 1996; C. Smith *et al.,* 1996; Miller *et al.,* 2000). In addition, deposit feeders' gut contents also exhibited enrichment of $^{234}Th_{xs}$ activity, chl *a*, and phaeopigments compared to surrounding sediments (Miller *et al.,* 2000). Therefore, the correlation between $^{234}Th_{xs}$ activity and chloropigments apparently occurs not only in quiescent bathyal sediments, but also in deposit-feeder guts (Miller *et al.,* 2000). The relationship between $^{234}Th_{xs}$ activity and chl *a* and phaeopigments suggests that $^{234}Th_{xs}$ activity may be a reliable tracer of freshly deposited phytodetritus in habitats such as the quiescent bathyal basins off California. Freshly deposited phytodetritus appears to be an important food source for deep-sea

deposit feeders, potentially supplying organic carbon and nitrogen and other nutritional components (Billet *et al.,* 1988; Miller *et al.,* 2000).

The negative correlation between sediment EHAA and $^{234}Th_{xs}$ activity suggests that the ingestion of $^{234}Th_{xs}$ activity-rich material is not keyed to EHAA content. This result is interesting because it is often speculated that deposit feeders, including those in the deep sea, are nitrogen-limited (e.g., Tenore, 1988; Taghon and Greene, 1990; Jumars *et al.,* 1990; White, 1993) and that the major source of nitrogen available to deposit feeders may be polymerized amino acids (Mayer *et al.,* 1988, 1995). The relatively low spatial variation in EHAA concentrations within and across basins (Table 1) suggests relatively constant availability of this potential food material, allowing deposit-feeder foraging to focus on other nutritional requirements.

The absence of a linear correlation between sediment ATP and $^{234}Th_{xs}$ activity also suggests that deposit feeders are not ingesting $^{234}Th_{xs}$-rich material solely for its microbial content. Microbes play a principal role in organic matter decomposition, and thus are often responsible for converting relatively refractory organic material into high quality food (i.e., microbial biomass) for deposit feeders (Craven *et al.,* 1986; Lopez and Levinton, 1987). In addition, sediment associated microbes form a large portion of the base of the benthic food chain and are highly digestible and nutritious to deposit feeders (Lopez and Levinton, 1987). Total microbial biomass may increase in response to the influx of new, organic-rich material, which can then be consumed by deposit feeders. However, in the case of recently deposited phytodetritus, microbes may compete with deposit feeders for this new labile food resource (C. Smith, 1994).

Our findings suggest that $^{234}Th_{xs}$ activity may be a reliable indicator of freshly deposited phytodetritus available to deep-sea deposit feeders in quiescent habitats, but is not indicative of amino acid-rich or microbe-rich material. Because deep-sea deposit feeder gut sediments typically are extremely enriched in $^{234}Th_{xs}$ activity, and $^{234}Th_{xs}$ activity is not positively correlated with microbial biomass or amino acids, our results provide no evidence that deep-sea deposit feeders select amino-acid-rich or microbial-rich sediments (nor do our results *disprove* such selectivity). Our findings *do,* however, suggest that deep-sea deposit feeders select phytodetritus for some other nutritional component, e.g., labile organic carbon, polyunsaturated fatty acids, and/or vitamins (Phillips, 1984).

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