Sediment community structure around a whale skeleton in the deep Northeast Pacific: Macrofaunal, microbial and bioturbation effects

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Abstract

Chemoautotrophic communities on lipid-rich whale skeletons are known from a total of 16 modern and fossil sites in the deep Pacific Ocean. While the attached fauna of modern whale bones has been studied, the impact of whale falls on surrounding sediment assemblages remains largely unevaluated. Using the research submersible *Alvin*, we sampled the sediment community at distances of 0, 0.5, 1, 2, 4, and ~ 100 m from the lipid-rich skeleton of a 21 m balaenopterid on the 1240 m seafloor in Santa Catalina Basin. When sampled in 1988 and 1991, the skeleton had been on the seafloor for > 4 yr and supported a large attached chemoautotrophic assemblage. Sedimentary organic content, microbial biomass and bacterial abundance were not significantly different near the skeleton than in background sediments, and pore-water sulfide concentrations were only modestly elevated (to $\leqslant 20 \, \mu M$) adjacent to the bones. The species composition of infaunal macrobenthos near the skeleton was similar to that in background sediments, providing little evidence of a specialized enrichment and/or sulfophilic assemblage. Nonetheless, macrofaunal abundance within 0.5 m of the skeleton was reduced by $> 40\%$, due to a decline in the paraonid polychaete *Levinsenia oculata*. The reduction in

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L. oculata (the community dominant) caused a sharp increase in rarefaction diversity near the skeleton. Bioturbation intensities, evaluated from ^{234}Th profiles, were also dramatically reduced in sediments near the skeleton, as were rates of extracellular lipase activity. We postulate that reduced infaunal abundance and bioturbation near the skeleton resulted from the interference effects of vesicomyid clam-shell debris, and that the low bioturbation rates in turn limited extracellular lipase activity. We conclude that whale skeletons, and the remains of their associated chemoautotrophic assemblages, may physically impact nearby sediment communities for years after the organic and sulfide enrichment effects of whale falls have dissipated, yielding changes in infaunal diversity and bioturbation. © 1998 Elsevier Science Ltd. All rights reserved.

1. Introduction

Unusual biotic communities are now known from eight naturally occurring lipid-rich whale skeletons in the deep North and South Pacific Oceans (Marshall, 1987, 1994; Gibbs, 1987; Smith et al., 1989; Fujioka et al., 1993; Bennett et al., 1994; Baco et al., 1996; Wada et al., 1994; Naganuma et al., 1996; Deming et al., 1997). Fossil whale-bone communities also have been described from eight deep Pacific whale skeletons dating from the Oligocene (Squires et al., 1991; Goedert et al., 1994). Both modern and fossil communities include dense, speciose assemblages of macro-invertebrates and bacterial mats attached directly to bone surfaces, as well as high densities of megafaunal mollusks in immediately underlying sediments (e.g. Bennett et al., 1994; Wada et al., 1994; Goedert et al., 1994; Naganuma et al., 1996; Baco et al., 1996). Many of the most abundant species, including mytilid, vesicomyid, lucinid, and thyasirid bivalves, depend on chemoautotrophic bacterial endosymbionts that utilize sulfide derived from the anaerobic decay of bone lipids as an energy source (Smith et al., 1989; Smith, 1992b; Bennett et al., 1994; Goedert et al., 1994; Deming et al., 1997). Other bone-community components include bacterial-mat grazers [numerous species of limpets (e.g. McLean, 1992; Bennett et al., 1994; Baco et al., 1996)] and specialized consumers of bone lipids [e.g. sipunculids (Gibbs, 1987) and lipolytic bacteria (Deming et al., 1997)]. Whale skeletons may thus contribute fundamentally to hard-substrate habitat diversity in the deep sea and facilitate the dispersal of sulfophilic species between sulfide-rich habitat islands, such as hydrothermal vents, cold seeps and anoxic basins (Smith et al., 1989; Bennett et al., 1994; Butman et al., 1995; Committee on Biological Diversity in Marine Systems, 1995).

While the epifauna of deep-sea whale bones [and even cow bones (Kitazato and Shirayama, 1996)] has received significant study, the fauna in sediments surrounding whale skeletons remains undescribed. We predict that a whale fall on the deep-sea floor should have four stages of impact on the surrounding sediment community, occurring in temporal succession.

1. The initial deposition of a whale carcass, in combination with the large aggregation of megafaunal scavengers certain to be attracted in any oxic site (e.g. Dayton and

Hessler, 1972; Isaacs and Schwartzlose, 1975; Hessler et al., 1978; Smith, 1985), should yield substantial resuspension of muddy deep-sea sediments (Smith, 1986; Grassle and Morse-Porteous, 1987). Such physical disturbance likely will cause reductions in macrofaunal community abundance and species diversity within a few meters of the whale carcass (cf. Smith, 1986).

2. The enormous mass of soft tissue on a whale carcass [> 10,000 kg wet weight for adults of the nine largest species of cetaceans (Lockyer, 1976)] will yield intense organic enrichment of the surrounding sediments in a generally organic-poor environment. Heterotrophic enrichment opportunists, for example bacterial mats, capitellid and dorvilleid polychaetes, cumaceans and leptostracans, are likely to colonize enriched sediments in large numbers (cf. Turner, 1977; Pearson and Rosenberg, 1978; Levin and Smith, 1984; Smith, 1985, 1986; Grassle and Morse-Porteous, 1987; Vetter, 1994, 1996; Snelgrove et al., 1996; Naganuma et al., 1996). Whale soft tissue also may attract endemic respondents, just as wood falls, seagrass accumulations, squid beaks, and bare whale bones appear to harbor their own specialists (Turner, 1973; Wolff, 1979; Gibbs, 1987; Marshall, 1987, 1994; Waren, 1989; McLean, 1992). Dense assemblages of opportunists should persist for at least as long as enrichment conditions, likely will yield local reductions in species diversity of macrobenthos, and will be associated with reduced rates and depths of bioturbation (cf. Turner, 1977; Pearson and Rosenberg, 1978; Grassle and Morse–Porteous, 1987; Levin et al., 1994).

3. Sulfides released from the anaerobic decay of whale soft tissue and bone lipid should foster an exotic assemblage of sulfide tolerant and sulfophilic microbes (e.g. *Beggiatoa* spp.) and metazoans living in surrounding sediments, including species with sulfur-oxidizing chemoautotrophic endosymbionts. Methane also may be released during whale tissue decay (Allison et al., 1991; Naganuma et al., 1996), fostering free-living or endosymbiotic bacterial methanotrophs. Such an assemblage might be expected to resemble those at sedimented hydrothermal vents, cold seeps and suboxic basins and slopes, and be characterized by low macrofaunal species diversity (Grassle et al., 1985; Grassle, 1988; Cary et al., 1989; Petrecca and Grassle, 1990; Tunnicliffe, 1991; Levin et al., 1994; Barry et al., 1996).

4. After an extended period of time (years to decades after whale-carcass deposition), whale soft tissue and lipids will have been consumed or decomposed; enrichment and sulfide impacts will then be restricted to sediments immediately underlying lipid-rich bones. At this stage, whale skeleton effects on the surrounding sediments should be largely limited to flow disruption to a distance of several bone diameters (~ 1–2 m) from the skeleton (Nowell and Jumars, 1984).

To begin to test these four predictions, we evaluated macrofaunal community structure, microbial biomass, bacterial abundance and extracellular lipase activity, sedimentary organic carbon content, and rates of bioturbation in sediments at various distances from the lipid-rich skeleton of a large balaenopterid at the bathyal seafloor in Santa Catalina Basin (SCB). When sampled in 1988 and 1991, this skeleton had been in place for 4–36 yr and harbored a substantial whale-bone community, including a large chemoautotrophic assemblage (Smith et al., 1989; Bennett et al., 1994).

Here we present the results of our sediment-community analyses. We find that during 1988–1991 the whale skeleton caused at most minor enrichment of nearby sediments; nonetheless it appeared to have depressed microbial lipase activity and bioturbation rates, and yielded an unexpected increase in local macrofaunal species diversity.
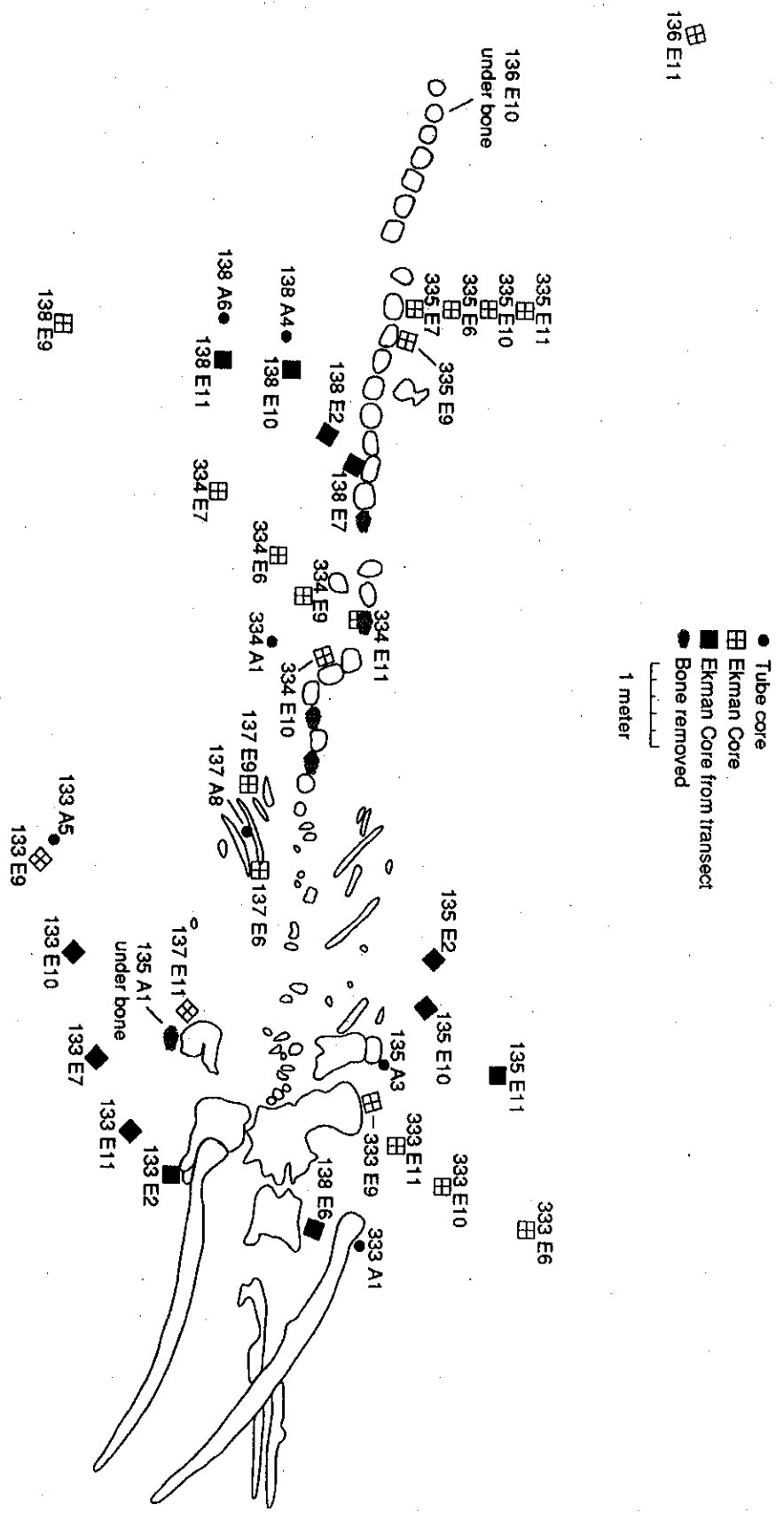
2. Study site and methods

2.1. Study site

The whale skeleton studied (Fig. 1) lies at a water depth of 1240 m on the level seafloor of the SCB at 33°12'N, 118°30'W [see Allison et al. (1991) for a map of the area]. This basin has been the site of intensive studies of carbon flux and benthic community dynamics over the past 16 yr [see references in K. Smith (1987), Kukert and Smith (1992), and Smith et al. (1993)]. Bottom-water oxygen concentrations at this site are 18–23 μM (Archer et al., 1989), and bottom water temperature and salinity are 4.1°C and 34.4‰, respectively (Emery, 1960). Surface sediments are a poorly sorted silty clay with a disaggregated median grain size of about 4.0 μm (Emery, 1960); *in situ* median grain size falls between 250 and 500 μm due to sediment pelletization by deposit feeders (Kukert and Smith, 1992). Sediment organic-carbon content is relatively high (3–6% by weight; Smith, 1986; DeMaster and Smith, unpublished data), and oxygen penetrates only to sediment depths of 5–10 mm (Archer et al., 1989); however, pore-water concentrations of free sulfide normally remain low (< 1 μM) to depths of 10 cm (Smith et al., 1989). For a detailed description of the SCB benthic habitat, see Smith and Hamilton (1983).

The whale skeleton studied is that of a blue or fin whale (*Balaenoptera musculus* or *B. physalis*), and was discovered on the seafloor by the research submersible *Alvin* in Nov. 1987 (Smith et al., 1989). At the times of this study (Nov. 1988 and Feb. 1991), the partially buried skeleton consisted primarily of mandibles, the cranial complex, humerus bones, a few eroded ribs, and numerous vertebrae (Fig. 1). The cranial complex and mandibles protruded up to ∼ 50 cm into the water column while the remaining bones protruded ∼ 10–30 cm. The larger bones, including vertebrae, humerus and ribs, had lipid-rich interiors, attaining lipid concentrations of > 60% by weight (Allison et al., 1991; Smith, 1992b; Deming et al., 1997). In 1988, significant amounts of free sulfide (3–20 μM) in the upper 10 cm of sediments were only detected within 10 cm of bones (Smith et al., 1989). Approximately, 50% of exposed skeleton surfaces were covered by bacterial mats, which included *Beggiatoa* sp. and other sulfur bacteria (Bennett et al., 1994; Deming et al., 1997). In addition, in 1988 and 1991 a large and diverse assemblage (> 12,000 individuals, > 42 species) of

Fig. 1. Whale skeleton map showing positions of samples from 1988 and 1991 listed in Table 1. The fist three digits of sample numbers correspond to the last three digits in *Alvin* dive numbers listed in Table 1 (i.e. 133 E2, corresponds to Ekman core 2 from *Alvin* dive 2133). Black squares denote Ekman cores used in macrofaunal transects.

Bone Emplacement Study

- Tube core
- Ekman Core
- Ekman Core from transect
- Bone removed

1 meter

N

136 E11

136 E10
under bone

335 E11
335 E10
335 E6
335 E7
335 E9

138 A6
138 A4
138 E11
138 E10
138 E2
138 E7
138 E9

334 E7
334 E6
334 E9
334 E11
334 A1
334 E10

137 E9
137 A8
137 E6

133 A5
133 E9
133 E10
133 E7
133 E11
133 E2

135 E2
135 E10
135 A3
135 A1
under bone
137 E11

333 E11
333 E9
138 E6
333 A1
333 E10
333 E6
135 E11

macro-invertebrates lived directly on the bones (Bennett et al., 1994). The dominant species, constituting 87% of the assemblage, were *Idas* (formerly *Idasola*) *washingtonia* [a mytilid with chemoautotrophic endosymbiont bacteria (Deming et al., 1997)], *Mitrella permodesta* (a gastropod), *Ilyarachna profunda* (an isopod crustacean), and three species of cocciliniform limpets (*Cocculina craigsmithi, Pyropelta corymba*, and *P. musaica*) (Bennett et al., 1994). In addition, sediments within 20 cm of the bones contained 400–800 megafaunal vesicomyid clams that are apparently dependent on sulfide-oxidizing, chemoautotrophic endosymbionts (Bennett et al., 1994; Deming et al., 1997). Among these dominant species, only *I. profunda* has been collected in background SCB sediments, where it is very rare (Bennett et al., 1994). See Bennett et al. (1994) and Baco et al. (submitted) for more detailed descriptions of the whale-bone epifaunal community and its relationship to vent-seep faunas.

2.2. Field methods

Sediment samples for macrofauna were collected with *Alvin* in Nov. 1988 along three transects running roughly outward from random points on the skeleton (Fig. 1; Table 1). Along each transect, one 20 × 20 cm Ekman box core (subdivided *in situ* into four 10 × 10 cm subcores) was collected with its nearest side at each of the following distances from the skeleton: 0 m (i.e. 1–2 cm from a major bone), ∼ 0.5, ∼ 1.0, ∼ 2.0 and ∼ 4.0 m. These sample distances were selected because they appeared to span the range of conditions from clam-shell littered sediments to undisturbed background sediments. For transect number 2135, the 0 m corer failed, so a makeup 0 m Ekman core (number 2138-E6) was collected at a nearby location. In addition, three Ekman cores were collected at random locations ∼ 100 m from the skeleton to sample the background community. Finally, two other Ekman core samples (2137-E11 and 2137-E6) were collected at distances of 0 and 0.5 m, respectively; these were processed but omitted from our transect analyses to preserve a balanced design. On deck, three subcores from each Ekman core were processed for macrofauna; the fourth subcore was sampled for ^{234}Th activity or other analyses (see below). Macrofaunal subcores were subsampled for microbiological analyses (removing 2–6% of the top 10 cm of sediment) and then extruded and sectioned into 0–1, 1–5 and 5–10 cm depth layers; depth layers were fixed whole in a borate-buffered 10% formalin/seawater solution.

To evaluate patterns of bioturbation around the skeleton, we measured sediment profiles of excess ^{234}Th (half-life = 24.1 d). Particles settling through the water column pick up an excess activity of ^{234}Th that can be used to trace particle behavior (e.g. particle displacement by animals, or bioturbation) for ∼ 100 d after particles have reached the seafloor (e.g. Smith et al., 1993). In 1988, we selected one 10 × 10 cm subcore from each of Ekman core numbers 2133-E7, 2133-E10, 2133-E11, and 2138-E7 for analysis of excess ^{234}Th (Table 1; Fig. 1). On shipboard, subcores were extruded, sectioned into 1 cm depth intervals, and processed as in Smith et al. (1993).

To evaluate sediment organic-carbon content around the whale skeleton in 1988, single cylindrical tube cores (each 35 cm^2 in area) were collected beneath a whale vertebra, at distances of 0, ∼ 0.5, ∼ 1.0, ∼ 2.0 and ∼ 4.0 m from the skeleton, and at two random locations ∼ 100 m from the skeleton (Table 1; Fig. 1). On shipboard,

Table 1

Samples collected for this study around the SCB whale skeleton in 1988 and 1991. BDC = bacterial direct counts; C_{org} = organic carbon; N_{org} = organic nitrogen

Sample type	ALVIN Dive no.	Date	Sample no.	Distance from skeleton (m)	Processed for
Ekman core	2133	11/88	E3	Under bone	BDC
			E2	0	Macrofauna, BDC, ATP
			E11	0.5	Macrofauna, Th-234, BDC, ATP
			E7	1.0	Macrofauna, Th-234, BDC, ATP
			E10	2.0	Macrofauna, Th-234, BDC, ATP
			E9	4.0	BDC, ATP
	2134	11/88	E2	~ 100 (BKGD)	BDC, ATP
	2135	11/88	E10	0.5	Macrofauna, BDC, ATP
			E2	1.0	Macrofauna, BDC, ATP
			E11	2.0	Macrofauna, BDC, ATP
	2136	11/88	E10	Under bone	BDC, ATP
			E11	4.0	BDC, ATP
			E2	~ 100 (BKGD)	Macrofauna
			E4	~ 100 (BKGD)	Macrofauna, BDC, ATP
			E7	~ 100 (BKGD)	Macrofauna, BDC, ATP
	2137	11/88	E11	0	Macrofauna
			E6	0.5	Macrofauna
			E9	0.5	BDC, ATP
	2138	11/88	E6	0	Macrofauna, BDC, ATP
			E7	0	Macrofauna, Th-234, BDC, ATP
			E2	0.5	Macrofauna, BDC, ATP
			E10	1.0	Macrofauna, BDC, ATP
			E11	2.0	Macrofauna, BDC, ATP
Tube core	2133	11/88	A5	4	C_{org}, N_{org}
	2134	11/88	A5	~ 100 (BKGD)	C_{org}, N_{org}
	2135	11/88	A1	Under bone	C_{org}, N_{org}, BDC, ATP
	2135	11/88	A3	0	C_{org}, N_{org}
	2136	11/88	A9	~ 100 (BKGD)	C_{org}, N_{org}
	2137	11/88	A8	0.5	C_{org}, N_{org}
	2138	11/88	A9	1.0	C_{org}, N_{org}
	2138	11/88	A6	2.0	C_{org}, N_{org}
Ekman core	2333	2/91	E9	0	Pore-water sulfide
			E11	0.5	BDC
			E10	1.0	BDC
			E6	2.0	BDC
			E7	~ 100 (BKGD)	Th-234
	2334	2/91	E10	0	BDC
			E11	0	BDC
			E9	0.5	Pore-water sulfide, BDC
			E6	1.0	BDC
			E7	2.0	BDC
	2335	2/91	E7	0	BDC
			E9	0	Pore-water sulfide
			E6	0.5	BDC
			E10	1.0	BDC
			E11	2.0	BDC

Table continued

Table 1. Continued

Sample type	ALVIN Dive no.	Date	Sample no.	Distance from skeleton (m)	Processed for
	2336	2/91	E9	~ 100 (BKGD)	Pore-water sulfide
			E11	~ 100 (BKGD)	BDC
Tube core	2331	2/91	A1	~ 100 (BKGD)	BDC
	2333	2/91	A1	0	BDC, Lipase
	2334	2/91	A1	0.5	BDC, Lipase
	2335	2/91	A1	~ 100 (BKGD)	BDC, Lipase

subsamples were taken from tube cores with 50 cc syringes modified into piston corers. Syringe cores were frozen at $-30°C$ and shipped to the laboratory for analyses.

In 1991, limited sampling was also conducted to evaluate free-sulfide concentrations in sediment pore waters at distances of ~ 0, ~ 0.5 and ~ 100 m from the skeleton (Table 1, Fig. 1). Pore-water samples were collected with a 10 cm diameter polycarbonate core liner fixed in the corner of an Ekman corer; the liner had sampling ports as described in Jahnke (1988). Shortly after Ekman core recovery, the entire polycarbonate liner and a Jahnke pore-water squeezing apparatus (Jahnke, 1988) were placed inside a nitrogen-filled glove bag and flushed with N_2 gas at least three times; positive N_2 pressure was maintained inside the glove bag throughout the squeezing process. Pore-water samples were removed through ports using the squeezer and 0.45 μm filters (Jahnke, 1988). To expel air from liner ports and sample filters, a few ml of pore water were allowed to drip from each filter before a syringe was attached. Pore waters were squeezed into syringes containing Cline's reagent (Cline, 1969) and thus immediately fixed. Sulfide concentrations were measured on shipboard with a Brinkmann Colorimeter using a 5 cm pathlength, a 670 nm wavelength filter, and appropriate standards.

Sediment samples for microbiological analyses were collected around the carcass in Nov. 1988 and Feb. 1991 with Ekman and tube cores (Table 1). These cores were subsampled on shipboard with 10 or 50 cc syringe piston cores. For determination of bacterial abundance by epifluorescence microscopy (described below) in both sampling years, syringe cores were sliced at intervals of 1–3 mm to a depth of 4 cm. A volume of 0.5 cc wet sediment from each interval was diluted 1 : 5 in 0.2 μm filtered sterile artificial seawater (ASW) containing 0.2 μm filtered 2% formaldehyde. Fixed samples were stored at 4°C in the dark for 1–2 months until processing in the laboratory. In our experience, short-term (months) storage of marine sediments does not result in reduced cell counts, as has been shown for seawater samples (Turley and Hughes, 1994). For measurement of microbial biomass by ATP extraction, separate subcores were extruded and sliced as for microscopic counts. Each sediment subsample was diluted 1 : 3 in 0.15 N nitric acid, processed as in Deming et al. (1979), and

frozen until further analysis in the laboratory (see below). In 1991, ATP samples were lost due to compromised shipboard reagents. Routinely, one subcore was processed per Ekman or tube core for both microscopic counts and ATP extraction; triplicate subcores were processed on several occasions to determine within-core variability.

Organic enrichment from a lipid-rich whale fall is expected to stimulate lipid degradation by sediment bacteria; we thus measured extracellular lipase activity around the skeleton, using methylumbelliferyl-butyrate as a lipid substrate. To measure lipase activity in relatively undisturbed sediments, replicate subcores were collected per dedicated tube core collected in Feb. 1991 near the skeleton (0 and 0.5 m) and in background sediments ($\sim$ 100 m). Methodology tests in 1988 determined the successful protocols used in 1991. All processing and analysis were done immediately on shipboard, using ice baths during preparations and a 4°C refrigerator for centrifugation and incubation steps. Six syringe piston cores, with side injection ports at 5 mm depth intervals, were used for a whole-core injection method adapted from Meyer-Reil (1986). Syringe cores were injected through each port, using a sterile Hamilton syringe, with 10 µl of 5 mM methylumbelliferyl (MUF)-butyrate. The MUF-butyrate was first dissolved in methylcellusolve, diluted to desired concentration in ASW, and degassed with nitrogen. Final mean concentration achieved in each sediment horizon would have been 50 µM, but substrate was distributed along a diffusive gradient, as described by Meyer-Reil (1986). Two subcores were sacrificed after each incubation interval of 0, 2 and 4 h (Relexans et al., 1996). At the end of each interval, subcores were sliced at 1 cm intervals, diluted in 3 ml ASW, and centrifuged 8 min at 2000 rpm. After buffering the supernates with Na borohydrate, fluorescence was determined in a Perkin–Elmer LS-5B spectrophotometer (excitation and emission wavelengths of 355 and 440 nm, respectively). Surface sediments (0–1 cm) from replicate subcores, taken from background and near-skeleton cores, were also diluted 1 : 10 in 0.2 µm filtered bottom water for the general slurry approach described by Mayer (1989). A final concentration of 10 µM MUF-butyrate was added to each slurry aliquot with subsequent processing as described above. Due to substrate gradients in the whole-core approach and homogeneous distributions in the slurry approach, direct comparisons of rates obtained by the two methods must be made with caution.

2.3. Analytical procedures

In the laboratory, macrofaunal samples were gently washed on a 425 µm sieve, transferred to 80% ethanol, and processed as in Kukert and Smith (1992). Individuals were identified to lowest possible taxon with the help of experts (particularly J. Blake, B. Hilbig and J. McLean). Abundance counts were based on the number of heads. Macrofaunal species and families were assigned to the functional groups *carnivores-scavengers-omnivores, surface-deposit feeders, subsurface-deposit feeders*, and *others*, using the criteria of Kukert and Smith (1992). For statistical analyses, the macrofaunal data from the three subcores within each Ekman core were pooled. Macrofaunal samples were sorted in sequence outward from the skeleton. By a distance of 2 m

from the skeleton, community structure had converged to that in background samples (based on statistical analyses described below), so the 4 m samples were not sorted.

We used nonparametric statistical tests to analyze macrofaunal results because the small number of replicates (3) created difficulties in testing for normality. Variations with distance from the skeleton in community abundance, species richness, individual species abundances and trophic-group abundances were analyzed using the Kruskal–Wallis test and *a posteriori* multiple comparisons (Siegel and Castellan, 1988), at an experiment-wise *alpha* level of 0.05. Patterns of species diversity were evaluated by tabulating mean rarefaction diversity (E_s) curves for the various sample distances, using the procedures of Hurlbert (1971) and Smith (1986). We calculated confidence limits for mean E_s curves using a t-distribution (Rosner, 1986; Smith, 1986). Significance of the trend of decreasing rarefaction diversity with distance from the skeleton was evaluated with Jonckheere's ordered alternatives test (Hollander and Wolfe, 1973).

To evaluate potential effects of vesicomyid clam-shell fragments on macrofaunal community structure, shell fragments were removed from each Ekman core sample during sorting for macrofauna and the dry mass measured gravimetrically.

In the laboratory, the 0–1, 1–2, 2–3, 4–5 and 7–8 cm levels of Ekman subcores selected for radiochemical analyses were assayed for excess ^{234}Th (Smith et al., 1993). Eddy-diffusive mixing coefficients were calculated from the excess ^{234}Th profiles, using the least-squares regression approach (Smith et al., 1993). Penetration depth for excess ^{234}Th in each profile was considered to be the minimum depth at which the regression line, or a data point, fell within one standard deviation (due to counting error) of zero activity.

For sediment organic and nitrogen analyses, the top 2 cm of frozen syringe cores were lyophylized, acidified with 30% HCl to remove carbonate, and dried to preserve soluble organic matter, pore-water ammonium and nitrate. A portion of the dried material was then weighed and combusted in quartz for 1 h at 850°C in the presence of purified cupric oxide wire and high purity granular copper, and carbon and nitrogen determined as in Macko et al. (1984).

Microscopic enumeration of bacteria in the fixed sediment samples was conducted with the dual-staining method of Deming et al. (1997). At least 20 fields or 200 bacteria were enumerated on each filter, using a Zeiss Universal Microscope and optical filters for acridine orange (AO) and DAPI. Switching between optical filters for AO and DAPI enabled a double check against non-bacterial, but AO-staining, particles. Numbers of bacteria were scaled to cm^3 of wet sediment, integrated to a depth of 4 cm (bacteria per cm^2), and analyzed according to core distance from the whale skeleton using the Kruskal–Wallis test.

ATP samples were thawed and assayed immediately in a Packard photometer, using DuPont luciferase buffered in 0.25 M Tris, pH 8.2, with 0.01 M magnesium sulfate and 0.001 M dithiothreitol. Equal volumes of enzyme and sample were used in the assay, along with appropriate standards and spiked sediment controls. The concentration of ATP was scaled to cm^3 of wet sediment, integrated to a depth of 4 cm (μg ATP per cm^2), and analyzed according to core distance from the skeleton. Because

our extraction method was not compared empirically to other methods, analysis was limited to site-specific patterns within this study.

For butyrate hydrolysis rates by the core injection method, fluorescence measurements were converted to butyrate concentration using standard curves and scaled to μg hydrolyzed per cm^3 wet sediment. Hydrolysis rates were calculated for each depth horizon by linear regression analysis ($n = 6$ in each case) and standard errors of resulting slopes were determined according to Sokal and Rohlf (1995). Hydrolysis rates by the slurry approach were determined and analyzed similarly, using the linear portion of the hydrolysis curve ($n = 12$ for the near-bone experiment; $n = 10$ for the background sediments). Slopes were tested for significant differences with the t-test (Sokal and Rohlf, 1995).

3. Results

3.1. Macrofaunal community patterns

A total of 143 species were distinguished in the 2649 macrofaunal individuals collected in our 17 Ekman cores in 1988. Seven of these species (Table 2) had not been collected during previous intensive sampling of sediment macrofauna in SCB (Jumars, 1976; Smith, 1986; Kukert and Smith, 1992), and thus might be considered "exotic" to the Basin. All seven potentially exotic species were extremely rare, constituting in

Table 2
Sediment macrofaunal species found near the whale skeleton that were not previously collected in SCB. Samples were $300\,cm^2$ from Ekman box cores. Each sample contained one individual of the indicated species, except 2138 E7, which contained two *Mitrella permodesta*. In the Taxonomic Group column, P = polychaete, and M = mollusk

| Species	Taxonomic group	Distance from skeleton (m)	Sample no.
Asclerocheilus sp. A	Scalibregmid (P)	0	2138 E6
Ephesiella brevicapita	Spaerodorid (P)	0	2133 E2
		0	2138 E6
		0.5	2138 E2
Harmothoe craigsmithi	Polynoid (P)	0	2133 E2
		0	2138 E6
		0.5	2138 E2
Ophryotrocha nr. *globopalpata*	Dorvilleid (P)	0	2137 E11
		0	2138 E7
		0.5	2137 E6
Sphaerosyllis sp. A	Syllid (P)	0	2137 E11
Mitrella permodesta	Gastropod (M)	0	2138 E6
		0	2138 E7
		0	2135 E 2
Golfingia nicolasi	Sipunculan	2	2138 E11
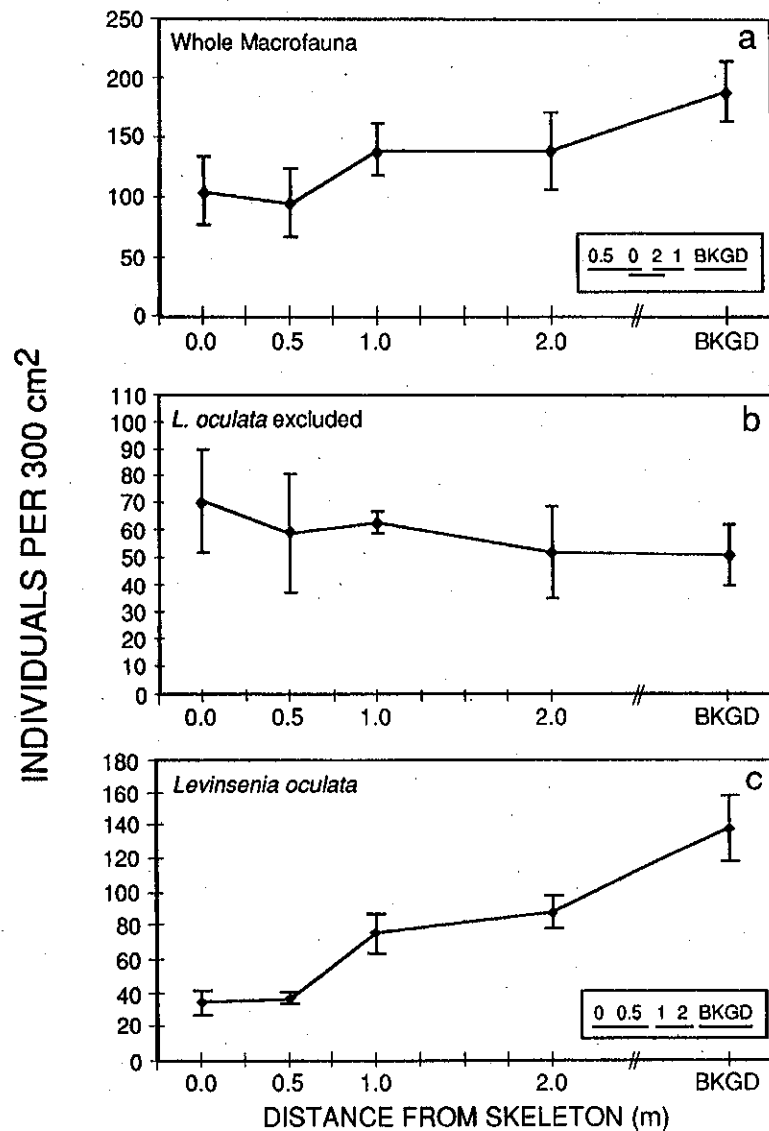
Fig. 2. Mean abundance as a function of distance of (a) the whole macrofauna, (b) macrofauna with *Levinsenia oculata* excluded, and (c) the paraonid polychaete *Levinsenia oculata*. Error bars are ± one standard error. Boxes in (a) and (c): Means at sample distances not sharing a common underline are significantly different at $p = 0.05$.

aggregate $< 1\%$ of the macrofauna collected around the skeleton. Six of these species were restricted to within 1 m of the whale skeleton, suggesting a response to habitat conditions created by the bones (Table 2). Only one of these exotic species (the snail *Mitrella permodesta*) was collected on the adjacent whale bones, where it was abundant (Bennett et al., 1994). Another of the exotic species (the polynoid polychaete *Harmothoe craigsmithi*) was new to science (Pettibone, 1993).

Mean macrofaunal community abundance was highest in the background samples, and declined with decreasing distance to the whale skeleton (Fig. 2). Mean community

abundance at 0 and 0.5 m from the skeleton was $\leqslant 56\%$ that in background samples; this difference was statistically significant (Fig. 2). The most abundant macrofaunal species at all distances from the whale skeleton was the paraonid polychaete *Levin-senia oculata*, which constituted 33–73% of mean total abundance (Table 3). Nonetheless, this species declined precipitously ($p < 0.02$, Kruskal–Wallis test) with decreasing distance to the whale skeleton; at 0 and 0.5 m the abundance of *L. oculata* was less than 25% that in background samples (Table 3 and Fig. 2). No other macrofaunal species exhibited significant changes in abundance with distance from the skeleton, with the next four most common species remaining relatively constant in mean abundance at all distances (Table 3).

Interestingly, the decline in total macrofaunal abundance near the whale skeleton was solely a consequence of the dwindling density of *L. oculata*. When *L. oculata* was excluded from the analysis, mean macrofaunal abundance did not change significantly with distance from the skeleton and, in fact, increased slightly adjacent to the bones (Fig. 2).

Of the four trophic groups analyzed (*carnivores-scavengers-omnivores, surface-deposit feeders, subsurface deposit feeders*, and *others*), two showed significant patterns around the whale skeleton. The mean abundance of *subsurface-deposit feeders* declined significantly at 0–0.5 m from the bones relative to background sediments ($p < 0.02$, Kruskal–Wallis test, Fig. 3); this three-fold decline resulted solely from near-bone reductions in *L. oculata*, which was the predominant subsurface-deposit feeder. In contrast, the average abundance of *carnivores-scavengers-omnivores* increased monotonically with approach to the skeleton. Because *total* macrofaunal abundance declined near the bones as the density of *carnivores-scavengers- omnivores* increased, this trophic group constituted on average only 3% of community abundance in background samples, but accounted for fully 16% adjacent to the bones (Fig. 3); this increase in relative abundance for *carnivores-scavengers-omnivores* was statistically significant ($p < 0.05$, Kruskal–Wallis test).

Macrofaunal species diversity exhibited a marked pattern around the whale skeleton. Species richness per number of individuals, expressed as rarefaction curves (Fig. 4a), increased monotonically with approach to the skeleton; this trend was statistically significant ($p < 0.05$, Jonckheere's test). At 50 individuals, the mean expected number of species at 0 m from the skeleton (24.5) was nearly twice that in the background community (12.9). Once again, this pattern was driven by *L. oculata*; when this species was excluded from the rarefaction analysis, rarefaction curves at all distances became nearly identical (Fig. 4b). Thus, as *L. oculata* became less dominant near the skeleton, the increased evenness in species structure caused rarefaction curves to rise. On an areal basis, species diversity did not change significantly with distance from the carcass (Fig. 4c).

3.2. Bioturbation patterns

All four profiles of excess [234]Th measured near the whale in 1988 were well fitted in the top 3 cm by regression lines, suggesting that near-surface mixing processes were
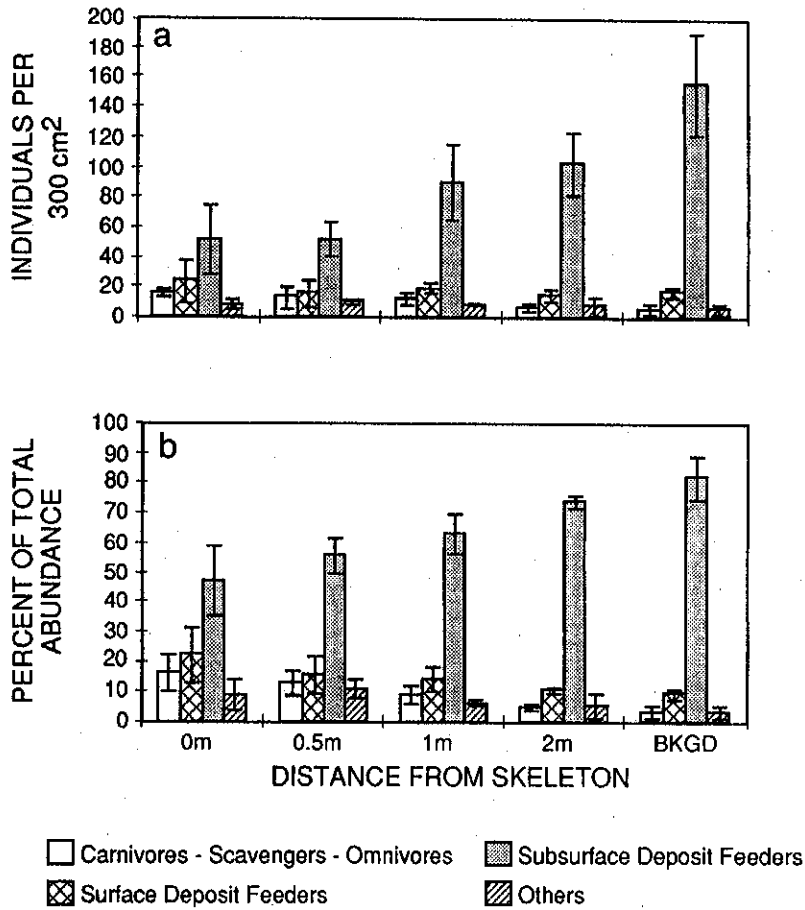
Table 3
Mean (± S.E.) abundance per 300 cm² core, and percent of total macrofaunal abundance, for the five dominant macrofaunal species sampled in 1988 around the whale skeleton

Species	Distance from whale skeleton (m)									
	0		0.5		1		2		Bkgd	
	No. per 300 cm²	Percent	No. per 300 cm²	Percent	No. per 300 cm²	Percent	No. per 300 cm²	Percent	No. per 300 cm²	Percent
Levinsenia oculata	35 ±8	32 ±4	37 ±4	40 ±4	76 ±12	53 ±3	88 ±9	64 ±3	139 ±20	72 ±5
Cossura sp. A	3.7±1.2	3.4±0.9	3.3±0.3	3.6±0.5	3.0±1.5	2.0±0.8	3.0±1.5	2.0±0.8	4.3±1.2	2.2±05
Tharyx monilaris	3.0±0.6	2.8±0.2	3.3±1.5	3.2±1.0	4.0±0.6	2.8±0.3	2.7±1.5	1.7±0.9	4.0±1.5	2.2±0.6
Exogone sp. A	4.0±0	4.0±0.7	5.7±2.9	5.2±2.2	6.3±0.9	4.5±0.2	3.0±1.5	1.9±1.0	3.3±1.5	1.9±0.8
Tharyx tesselata	3.0±1.0	2.6±0.6	4.0±1.5	3.8±1.2	4.7±1.2	3.7±1.0	1.3±0.9	0.9±0.5	3.0±1.2	1.7±0.7

Fig. 3. Mean absolute and per cent abundance of macrofaunal functional groups with distance from the whale skeleton. Error bars are ± one standard error.

well approximated by eddy diffusion (Fig. 5). The resultant diffusive mixing coefficients and penetration depths for excess ^{234}Th varied little over distances of 0–2 m from the skeleton. However, when taken as a group, the diffusive mixing coefficients from ≤ 2 m from the skeleton were substantially (and significantly) smaller than those measured for ^{234}Th in nearby background sediments by Smith et al. (1993) and Pope (1996); the mean near-skeleton coefficient was ~ 1/20 that in background sediments (Table 4). The mean penetration depth of excess ^{234}Th within 2 m of the skeleton was also less than 1/2 that in background sediments (Table 4). We conclude that, on the 100 d time scales of excess ^{234}Th, bioturbation rates within the 2 m of the skeleton were dramatically lower in 1988 than in SCB background sediments in 1984–1991.

3.3. Sedimentary parameters

The percentage of organic carbon and the C/N ratio of organic matter in near-surface sediments showed no systematic pattern around the whale skeleton in 1988
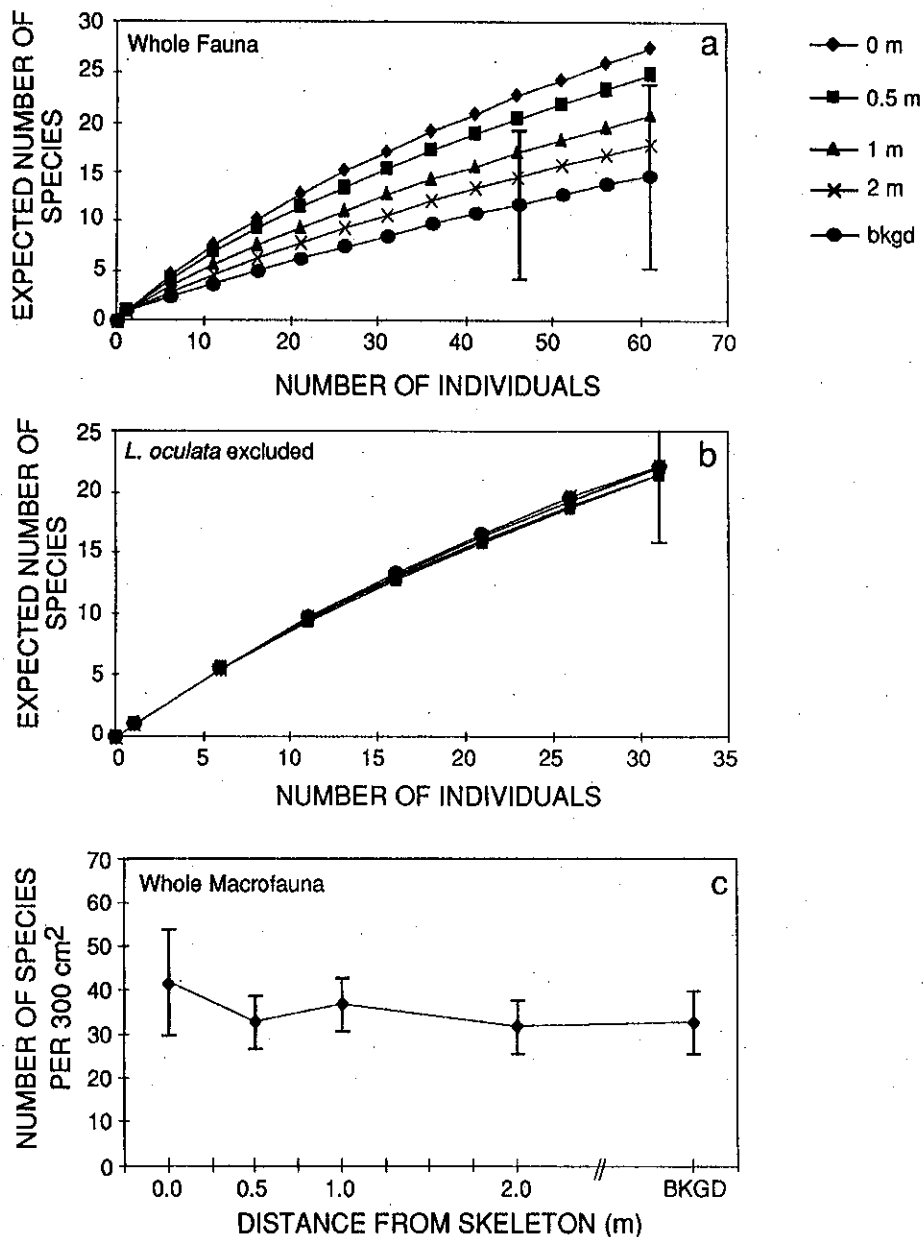
Fig. 4. Macrofaunal species diversity around the whale skeleton. (a) Hurlbert rarefaction curves for the whole macrofauna at distances of 0, 0.5, 1, 2 and ∼ 100 m (BKGD) from the skeleton. Error bars are 95% confidence limits for the BKGD curve, based on the t-distribution. (b) Hurlbert rarefaction curves as in (a) with *Levinsenia oculata* excluded from the fauna. Error bars are 95% confidence limits for the BKGD curve. (c) Number of species per 300 cm² as a function of distance from the whale skeleton. Error bars are ± one standard error.

(Fig. 6). Thus, there was no evidence of organic enrichment of sediments in the vicinity of the skeleton.

Pore-water sulfide concentrations were very low in the top 5 cm of sediment (not exceeding 1 μM) at all distances from the whale skeleton sampled in 1991 (Table 5). In
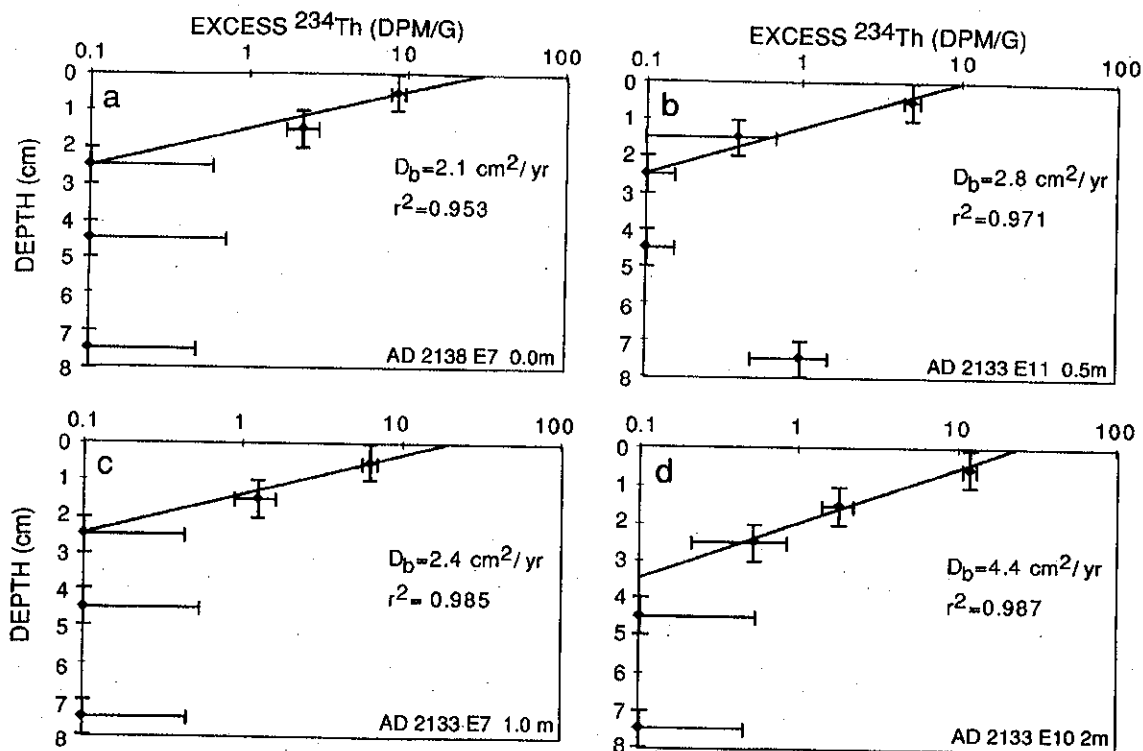
Fig. 5. Profiles of excess ^{234}Th activity versus sediment depth at various distances from the whale skeleton in 1988. The indicated eddy diffusion coefficients (D_b) and r^2 values are derived from the regression lines, as detailed in Smith et al. (1993). Sample number and distance from the whale skeleton are indicated in the lower right of each panel. Error bars are ± one standard error due to counting statistics.

the 0.5 m and background samples, sulfides remained low to the bottom of cores (14 cm). Immediately adjacent to whale bones, free sulfide levels tended to increase modestly at depths > 5 cm, reaching a maximum of ~ 10 μM at 15 cm in one core. These very limited data suggest that free-sulfide levels in surficial SCB sediments were generally very low, but were modestly enhanced in some areas within one core diameter (10 cm) of the whale skeleton.

Clam shell fragments were most abundant in sediments adjacent to the whale skeleton (Table 6); by a distance of 1 m, the average weight of clam shells collected per 300 cm^2 of sediment had fallen to near zero. Thus, any structural influence of shell fragments was restricted to within 1 m of the skeleton, and most pronounced within 0.5 m.

3.4. Patterns of microbial biomass, bacterial abundance and lipase activity

In 1988, neither sedimentary microbial biomass (measured by ATP extraction, Fig. 7a) nor bacterial abundance (microscopic counts, Fig. 7b) exhibited a statistically significant pattern with distance from the skeleton. The mean ATP value in background sediments was large relative to points nearer the skeleton, and mean ATP levels under bones were somewhat higher than at distances of 0–2 m; however, high

Table 4

Eddy diffusive mixing coefficients (D_b) and penetration depths for excess ^{234}Th in sediments near the whale skeleton and in the SCB background community. Mean mixing coefficients and mean penetration depths were significantly smaller within 2 m of the skeleton than in background sediments ($p < 0.005$, two-tailed Mann–Whitney tests). Background data are from Smith et al. (1993) and Pope (1996)

Distance from skeleton (m)	Sample no.	Date collected	D_b (cm^2/yr)	Penetration depth (cm)
Near skeleton				
0	2138 E7	11/88	2.1	2.5
0.5	2133 E11	11/88	2.8	2.5
1.0	2133 E7	11/88	2.4	2.5
2.0	2133 E10	11/88	4.4	3.5
			Mean = 2.9	Mean = 2.8
			S.E. = 0.5	S.E. = 0.25
Background				
100–400	1491 AC2	11/84	45	6
100–400	1777 E2	12/86	200	6
100–400	1789 E3	1/87	21	6
∼ 1500	RUMIII E4A	8/87	34	5.5
∼ 1500	RUMIII E4C	8/87	53	6.5
100–400	1934 E9	10/87	7.9	4.5
∼ 100	2333 E7	2/91	15	5
			Mean = 53.7	Mean = 6.1
			S.E. = 25.1	S.E. = 0.6
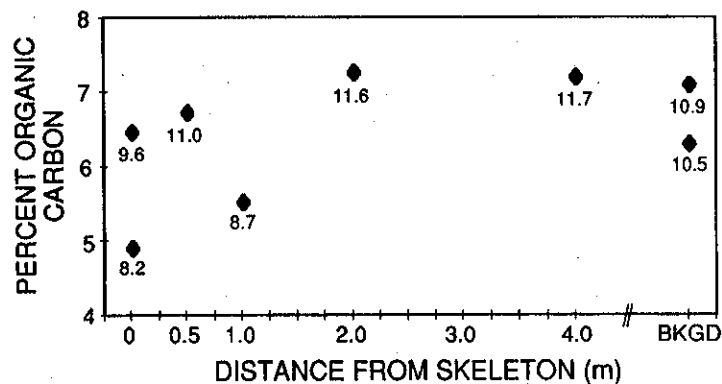
Fig. 6. Percent sedimentary organic carbon (dry weight), and C/N ratios of organic matter (numbers below points), in the top 2 cm of sediment versus distance from the whale skeleton in 1988.

within-core variability in the background (S.E. = 30% of mean, $n = 3$) and under bones (S.E. = 70% of the mean, $n = 3$) precluded statistical significance. Direct bacterial counts, integrated over a sediment depth of 4 cm, ranged from 1.1×10^9 to 1.0×10^{10} cells per cm^2, with both extremes coming from background sediments

Table 5

Pore-water sulfide concentrations (μM) at various depths in core samples collected around the SCB whale skeleton in 1991. Values of < 0.4 indicate that sulfide concentrations were measured but fell below the detection limit of 0.4 μM. Dashes indicate levels at which measurements were not made, due to absence of ports in core tubes (variable core penetration prevented uniform positioning of ports relative to the sediment-water interface)

Sediment depth (cm)	Distance from whale skeleton (m)			
	0 (AD 2333 E9)	0 (AD 2335 E9)	0.5 (AD 2334 E9)	Background (AD 2336 E9)
1	< 0.4	—	< 0.4	< 0.4
2	< 0.4	—	0.9	0.4
3	< 0.4	—	—	0.4
4	< 0.4	—	0.7	0.7
5	—	< 0.4	—	—
6	< 0.4	< 0.4	1.4	0.5
7	—	1.7	—	—
8	< 0.4	2.6	—	0.8
9	—	2.0	—	—
10	1.7	—	1.0	—
11	—	1.2	—	—
12	—	—	0.9	—
13	—	2.2	—	—
14	—	—	0.6	0.9
15	—	10.1	—	—

Table 6

Dry weight of vesicomyid clam shell fragments per 300 cm^2 at various distances from the whale skeleton. At all distances, $n = 3$

Distance from skeleton (m)	Mean dry weight (g) $\pm$ S.E.
0	17.7 $\pm$ 8.3
0.5	7.0 $\pm$ 4.0
1.0	0.15 $\pm$ 0.10
2.0	0.14 $\pm$ 0.14
4.0	0
Background ($\sim$ 100 m)	0

(Fig. 7b). Although three of the four highest bacterial counts were found beneath whale bones, the high background count rendered any trend nonsignificant ($p > 0.10$, Kruskal–Wallis test). In 1991, direct counts of sedimentary bacteria again showed no significant change in bacterial abundance with distance from the whale skeleton ($p > 0.10$, Kruskal–Wallis test, Fig. 7c). In addition, counts at all distances from the skeleton in 1991 were roughly similar to those in 1988, yielding no evidence of substantive change in bacterial abundance between 1988 and 1991.
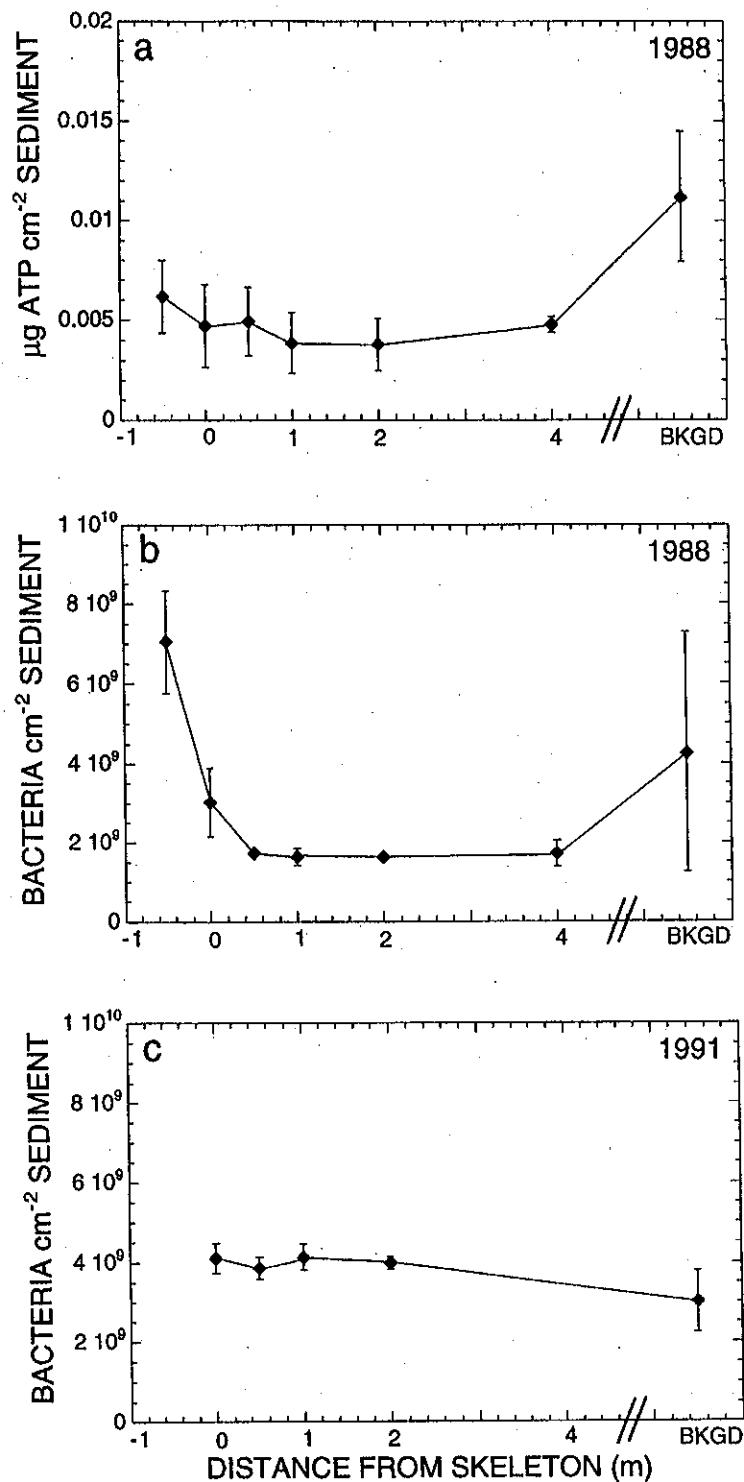
Fig. 7. Mean depth-integrated values of (a) sedimentary microbial biomass (by ATP extraction) in 1988 versus distance from the skeleton. Mean depth-integrated sedimentary bacterial abundance (by epifluorescence microscopy) in 1988 (b) and 1991 (c) versus distance from the skeleton. Values plotted at a distance of ~ 0.3 m were from samples taken under bones. Bars indicate ± one standard error (*n* = 3 or 4 in all cases). All values were integrated to a sediment depth of 4 cm.
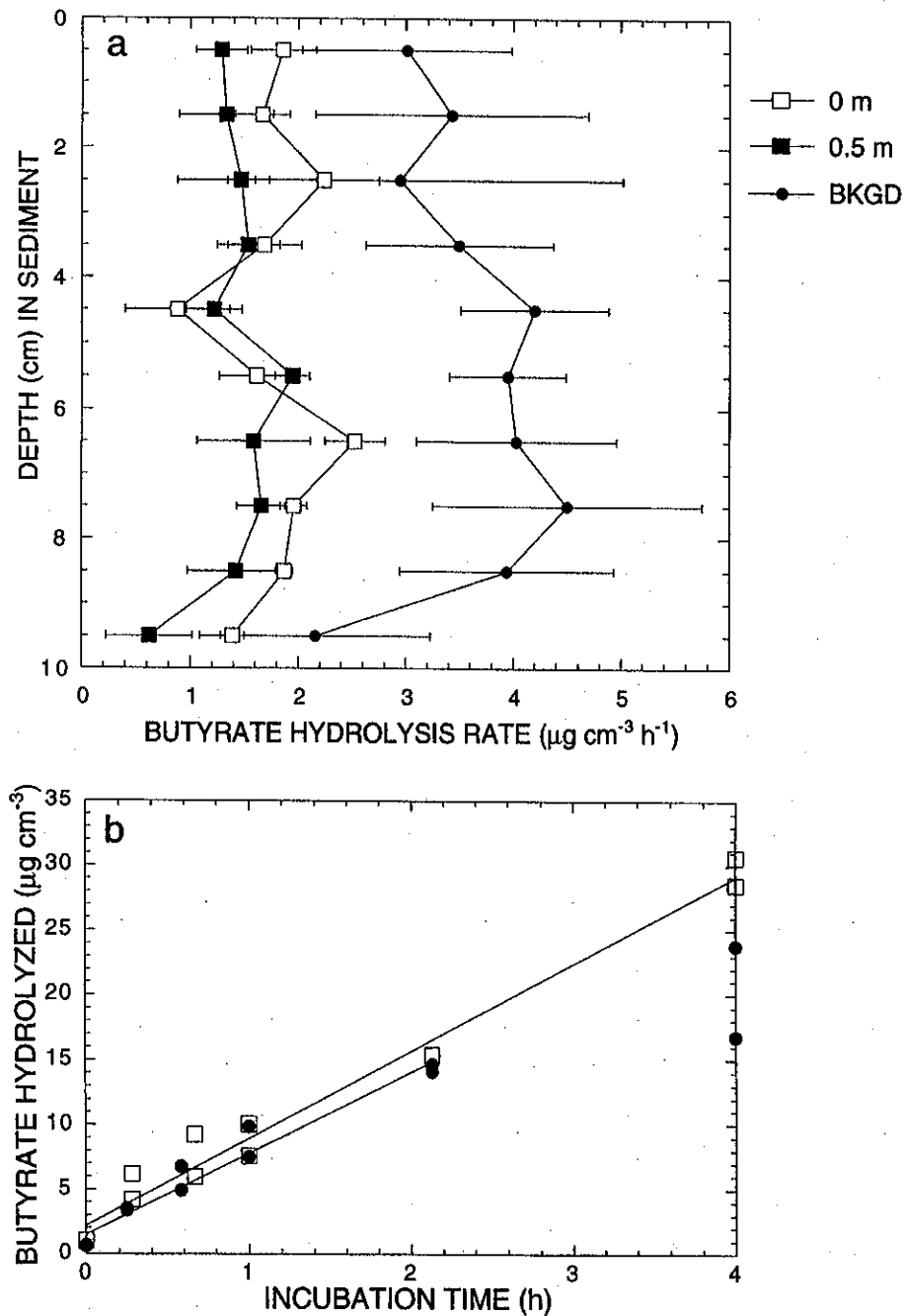
Fig. 8. Rates of lipolytic activity in sediments (using MUF-butyrate as a lipid substrate analog) versus distance from the skeleton measured in 1991 with (a) the core injection method and (b) the slurry method. Bars in (a) indicate ± one standard error of the slope for each experimental rate determination ($n = 6$ at each point).

In contrast to measurements of microbial biomass and bacterial abundance, assays of extracellular lipase activity in 1991 exhibited marked differences with distance from the whale skeleton. Rates of butyrate hydrolysis in sediments, measured with whole-core injection, were approximately two-fold higher in background sediments

than at distances of 0 and 0.5 m from the skeleton (Fig. 8a). However, lipase potential, as measured by butyrate hydrolysis rates in sediment *slurries*, showed no significant difference between 0 m and background sediments (6.74 versus 6.23 $\mu g \, cm^{-3} \, h^{-1}$; $p > 0.05$ with slope standard error test; Fig. 8b). Thus, *in situ* rates of lipase activity appeared to be lower in sediments adjacent to the skeleton, while the *potential* for lipase activity appeared to be unaffected.

4. Discussion

During 1988–1991 sediment community parameters exhibited varying responses to the presence of the SCB whale skeleton. Responses ranged from no significant skeleton impact (e.g. on sediment organic carbon content and microbial standing crop), through weak, decimeter-scale effects (e.g. on pore-water sulfides, lipase activity and the presence of exotic species), to intense, meter-scale influences (e.g. changes in macrofaunal abundance, diversity, and the rates and depths of bioturbation). Below we discuss the causality and significance of these whale skeleton effects in order of increasing intensity and spatial scale.

Sediment organic carbon, nitrogen content, and C/N ratios showed no systematic variation with distance from the whale skeleton, suggesting that any organic enrichment of the seafloor by whale soft tissue or bone lipids had dissipated by 1988. The absence of sediment-enrichment effects is consistent with the lack of marked change in microbial biomass or bacterial abundance around the skeleton because organic enrichment is typically associated with increased microbial standing crop (e.g. Pearson and Rosenberg, 1978; DeFlaun and Mayer, 1983). It should be noted, however, that SCB background sediments are high, by deep-sea standards, in both organic-carbon content (e.g. Smith et al., 1983) and microbial standing crop (see Deming and Baross, 1993; Relexans et al., 1996); thus, subtle enrichment effects may have been obscured in sediments around the whale.

In agreement with very limited sulfide-electrode studies in 1988 (Smith et al., 1989), whale-skeleton enhancement of pore-water sulfides in 1991 was very weak (maximum concentration $\sim 10 \, \mu M$ at 15 cm sediment depth), patchy, and restricted to within 10 cm of whale bones. Evidently, sulfide flux from whale bones into the sediment was small and occurred only within a decimeter of the bones. The minimal perturbation to pore-water sulfide concentrations in sediments surrounding the skeleton was consistent with an absence of organic enrichment in 1988–1991.

Pore-water sulfide concentrations around the SCB skeleton ($< 20 \, \mu M$) were very low relative to those in sediments supporting chemoautotrophic assemblages at deep-sea cold seeps and hydrothermal vents. For example, at Monterey Canyon seeps, Barry et al. (1996) found pore-water sulfide concentrations of 90–11,300 μM, and concentrations in Guaymas Basin hydrothermal sediments exceeded 1000 μM (Von Damm et al., 1985).

As might be expected under these low enrichment and low-sulfide conditions, a specialized enrichment and/or sulfophilic macrofaunal assemblage appeared to be, at best, poorly developed in sediments around the whale bones in 1988. We did collect

seven macrofaunal species potentially exotic to SCB in cores near the skeleton, but all these species were extremely rare, constituting < 1% of the macrofauna sampled near the skeleton (Table 2). At least one of these species, *Golfingia nicolasi*, is common in oxygenated sediments in other California Basins (Thompson, 1980) and is very unlikely to be a sulfophile or enrichment respondent. Two other of our exotic species very likely are sulfophiles: the snail *Mitrella permodesta*, which lives in abundance directly on the SCB whale skeleton, in anoxic Santa Barbara Basin sediments, and at sulfide seeps in Monterey Canyon (Cary et al., 1989; Bennett et al., 1994; Barry et al., 1996); and the dorvilleid polychaete *Ophryotrocha* nr. *globopalpata*, which is very similar or identical to a species living in sediments at hydrothermal vents on the Juan de Fuca Ridge (J. Blake, pers. comm.; Tunnicliffe, 1991). The remaining four exotic species (Table 2) could well be either sulfophiles or organic-enrichment respondents, but their ecology is too poorly to known make a strong argument. The polynoid *Harmothoe craigsmithi* has only been reported from the SCB whale skeleton (Pettibone, 1993), so it may be a whale-fall endemic. Interestingly, the paucity of an exotic sulfophilic macrofauna in near-bone sediments contrasts dramatically with the situation on the whale bones themselves, which in 1988, 1991 and 1995 harbored a large and speciose assemblage of macrofaunal sulfophiles with affinities to the faunas of hydrothermal vents and cold seeps (Bennett et al., 1994; Baco et al., 1996; Deming et al., 1997). We conclude that in 1988–1991 a sulfide-rich habitat occurred only for those animals in direct contact with the SCB whale skeleton. The presence of a large population of megafaunal vesicomyids clams in sediments within 20 cm of the skeleton in 1988–1995 (Bennett et al., 1994; Baco et al., 1996) probably reflects the clams' abilities to exploit sulfide flux at the interface between bones and sediments.

The paucity of an exotic macrofauna in sediments surrounding the well-developed SCB whale-bone chemoautotrophic assemblage also contrasts dramatically with the situation at sedimented hydrothermal vents and cold seeps. At vents and seeps quantitatively sampled for sediment infaunal macrobenthos, adjacent sediments typically are inhabited by high densities and low diversities of species not found in non-chemoautotrophic habitats (e.g. Grassle et al., 1985; Grassle, 1989; Petrecca and Grassle, 1990), i.e. sediment community structure at vents and seeps is profoundly altered from "background" deep-sea conditions. This is undoubtedly because the sediment flux of reduced chemicals (e.g. sulfide, methane, petroleum hydrocarbons) is much higher in many vent and seep sediments than it was near the SCB whale skeleton in 1988–1991.

Microbial lipase activity, as measured by butyrate hydrolysis, exhibited a decline near the skeleton; this decline is further evidence that any sediment-enrichment effects from the whale fall had dissipated by 1991, because lipid enrichment of sediments is expected to *stimulate* microbial lipase activity. We postulate that this decline in lipase activity near the bones resulted from the relatively low rates of bioturbation around the skeleton, because sediment mixing controls the encounter rate between solid-phase enzymes and substrates, and this encounter rate in turn controls the measured rate of substrate hydrolysis (Vetter and Deming, 1994). In undisturbed sediments, enzyme and substrates frequently are associated with the solid phase (Mayer, 1989). As expected based on this hypothesis, *potential* lipase activity (as measured in

physically disturbed sediment slurries that maximize enzyme-substrate encounter) showed no difference with distance from the skeleton.

The decline in macrofaunal abundance within 0.5 m of the whale skeleton in 1988 is intriguing because it appears to result wholly from reduction in the density of a single species, the paraonid polychaete *Levinsenia oculata*. This indicates extreme sensitivity of *L. oculata* to conditions near the skeleton, in apparent contrast to most of the macrofaunal community. Possible causes of *L. oculata* reductions near the skeleton include: (1) avoidance of past (or current slight) conditions of organic or sulfide enrichment in near-bone sediments; (2) clam-shell interference with burrowing by *L. oculata*; (3) enhanced predation on *L. oculata* near the bones; and (4) "avoidance" by *L. oculata* (due to lower recruitment or postlarval emigration) of modified flow conditions near the bones. In an earlier study in SCB, *L. oculata* was attracted to baitfalls placed on the deep-sea floor (Smith, 1986), so we think it unlikely that *L. oculata* would differentially avoid enrichment conditions around the skeleton. In addition, *L. oculata* is considered to be a burrowing subsurface deposit feeder (Kukert and Smith, 1992), so it is unlikely to be unusually sensitive to modified flow. In contrast, both clam-shell interference and enhanced predation are realistic possibilities because of the increased abundance of shell fragments, and of the *carnivore-scavenger-omnivore* functional group, within 0.5 m of the skeleton. Clam-shell interference is perhaps the most tenable hypothesis because paraonids (including *L. oculata*) in the nearby San Diego Trough have been shown to be negatively correlated with solid structures (large cirratulid mud balls) protruding into the sediment (Jumars, 1975). If clam-shell debris is the cause of *L. oculata* reductions, this effect is likely to persist for years because clam shells were visibly abundant around the skeleton in 1988, 1991 (Bennett et al., 1994), and 1995 (unpublished data).

It should be noted that the *L. oculata* reduction around the whale skeleton is one of several examples of paraonid response to patchiness at the deep-sea floor. As mentioned above, *L. oculata* was attracted to baitfalls (Smith, 1986), and paraonids as a group were negatively correlated with cirratulid mudballs in the bathyal northeast Pacific (Jumars, 1975); in the northwest Arabian Sea, paraonid abundance was postively correlated with cirratulid mudballs (Levin and Edesa, in press). In addition, the abundance of *L. oculata* was differentially reduced in artificial and natural sediment mounds in SCB, presumably due to unusual sensitivity to burial disturbance (Kukert and Smith, 1992; Smith and Kukert, in prep.). At bathyal depths in the northwest Atlantic, a closely related paraonid (*Levinsenia gracilis*) has exhibited enhanced abundance in sediment pits and another (*Aricidea quadrilobata*) was enhanced under organic-enrichment conditions (Schaff and Levin, 1994). We hypothesize that many paraonids may be especially sensitive to habitat patchiness at the deep-sea floor.

The increase in absolute and relative abundance of the trophic group *carnivores-scavengers-omnivores* adjacent to the whale skeleton may reflect enhanced food resources for this functional group. The whale-skeleton epifaunal assemblage, and the vesicomyid population living adjacent to the bones (Bennett et al., 1994) are rich potential sources of prey items and/or carrion. The presence of clam shell fragments (Table 6) and empty *M. permodesta* shells in sediments adjacent to the bones (Bennett et al., 1994) suggests that portions of the chemoautotrophic bone

assemblage are indeed consumed, either as live prey or carrion, within the sediment community. It should be noted, however, that the *carnivores-scavengers-omnivores* constitute, at all distances, a small percentage of the macrofaunal community ($\leqslant 16\%$), so any enhancement effects from chemoautotrophic production appear to be small.

The increase in macrofaunal rarefaction diversity adjacent to the whale bones (Fig. 4) is remarkable due to its size and cause. Local diversity in SCB background sediments is low by deep-sea standards, whereas diversity adjacent to the whale skeleton (25 species per 50 individuals) rivals that in some of the most diverse deep-sea communities, such as the San Diego Trough (Jumars and Gallagher, 1982). Perhaps even more remarkably, this dramatic change in local diversity in SCB appears to result from the diminution (i.e. disturbance) of a single species, the community dominant *L. oculata*. As discussed above, the disturbance to *L. oculata* may result from shell interference with burrowing behavior. Whatever the cause, this result is consistent with the findings of Kukert and Smith (1992) that disturbance can enhance local rarefaction diversity in SCB by depressing abundance of the background community dominants. However, the increased rarefaction diversity near the skeleton occurred in the absence of any apparent enhancement of rare species (Fig. 4), in contrast to the normal predictions of the intermediate disturbance hypothesis (Connell, 1978; Petraitis et al., 1989). Our results highlight the importance of understanding individual species responses for interpreting the effects of pertubations on community-level parameters, such as rarefaction diversity.

The most intense and large-scale effect of the whale skeleton was an apparent reduction in bioturbation rates and depths for ^{234}Th within 2 m of the skeleton (Table 4). Because ^{234}Th has a half-life of only 24 d, reduced bioturbation near the skeleton must have occurred in the ~ 100 d prior to our Nov. 1988 cruise (e.g. Smith et al., 1993). Bioturbation rates and depths in the deep sea, including the SCB, are thought to be controlled by the feeding activities of megafaunal and macrofaunal deposit feeders (e.g. Wheatcroft et al., 1990; Smith, 1992a); Can observed faunal reductions explain the 20-fold decline in bioturbation coefficients around the whale skeleton? Bennett et al. (1994) found the abundance of epibenthic megafauna in 1988 to be only 30% lower within 1 m of the skeleton than in the background community; because biodiffusion coefficients scale directly to animal abundance (Wheatcroft et al., 1990), this megafaunal reduction seems far too small to explain the 20-fold change in biodiffusion coefficients. Large reductions in macrofaunal abundance around the whale were restricted to the subsurface deposit feeder *L. oculata*, which declined by 37–75% within 2 m of the skeleton; if *L. oculata* were the primary sediment mixer, this decline should again explain no more than a four-fold reduction in bioturbation coefficients. It is unlikely that the large vesicomyid clams were responsible for the 2 m halo of reduced bioturbation around the skeleton; in 1988 and 1991, these clams were only found within 20 cm of bones (Bennett et al., 1994). We thus suspect that a keystone sediment mixer, poorly censused by our coring and photographic techniques, was dramatically reduced in abundance near the whale skeleton; a likely candidate is the burrowing holothurian *Chiridota pacifica* (Smith, 1992a). We postulate that large active burrowers, such as *C. pacifica*, may have avoided near-skeleton

sediments due to the sediment "armoring" effects of buried clam-shell fragments. Because shell fragments were common around the skeleton from 1988 to 1995 (Bennett et al., 1994; unpublished observations), such an armoring effect could persist for years.

Naganuma et al. (1996) studied sediment-community parameters around the skeleton of a ∼ 14 m long Bryde's whale (*Balaenoptera edeni*) estimated to have been at the northeast Pacific seafloor (on the Toroshima Seamount, 4037 m depth) for at least 2–1 6 yr. As for the SCB skeleton, the lipid-rich bones of the Bryde's whale were encrusted with a large chemoautotrophic assemblage including bacterial mats, mytilid mussels (*Idas* sp.), and galatheids. Naganuma et al. found strong enrichment of fatty acids, thiosulfate-oxidizing enzyme activity, and autotrophic and heterotrophic bacteria in sediments directly beneath a single bone studied; these parameters also showed modest, patchy enhancement to distances of 1.5 m from the skeleton. In contrast, sulfide concentrations were enhanced to moderate levels ($< 20 \ \mu M$) only directly under the bone. Thus, in consonance with our findings, the Toroshima skeleton supported a large chemoautotrophic community directly in contact with the bones while causing only modest chemical and bacterial impacts on the surrounding sediment community.

The overall sediment community structure at the SCB whale skeleton in 1988–1991 most closely matched our hypothesized impact stage four (see Introduction), in which enrichment and/or sulfide effects from the whale fall are essentially restricted to sediments underlying lipid-rich bones. Results from Naganuma et al. (1996) suggest that the Toroshima whale fall was near the boundary between stages three and four, i.e. at a point where the sulfide and organic-rich halo from the carcass has dissipated from surrounding sediments. Based on these findings, our successional stage four occurred around both skeletons at least 2–4 yr after the whales' initial deposition (Bennett et al., 1994), consistent with our prediction of a development time for stage four of years to decades. In contrast to our expectations, this stage in SCB was associated with enhanced macrofaunal rarefaction diversity, and dramatically reduced rates of bioturbation and extracelluar lipase activity in nearby sediments, perhaps due in part to physical effects (e.g. presence of vesicomyid shell fragments) of the whale-fall chemoautotrophic community. Additional studies of whale-skeleton assemblages, and their influence on surrounding sediment habitats, are required (a) to determine whether these perturbations to infaunal diversity, bioturbation, and extracellular enzyme activity are characteristic of the latter stages of whale-fall community succession, and (b) to test our predictions of succession around whale carcasses more thoroughly.

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