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Control of deep-sea benthic community structure by oxygen and organic-matter gradients in the eastern Pacific Ocean

by Lisa A. Levin[1], Cynthia L. Huggett[1,2] and Karen F. Wishner[3]

ABSTRACT

At boundaries of oxygen minimum zones (OMZs), bathyal faunas experience steep gradients in oxygen and organic-matter availability. The present study compares changes in microbial, meiofaunal, macrofaunal and megafaunal benthic assemblages along these gradients on Volcano 7, a 2.3-km high seamount in the eastern tropical Pacific. Faunal tolerance to dysaerobic (low oxygen) conditions varies with organism size; microbial and meiofaunal abundances are less affected than macro- and megafaunal abundances. At the exceedingly low concentrations (< 0.1 ml/l) encountered on the upper summit of Volcano 7, oxygen appears to exert primary control over abundance, composition and diversity of macrofauna, overriding other factors such as food availability and sediment grain size. When oxygen concentration is sufficient, food availability in sediments (indicated by the presence of labile material such as chlorophyll *a*) is highly correlated with meiofaunal and macrofaunal abundance.

Four distinct physical zones were identified on Volcano 7: (1) the coarse-grained upper summit zone (730–770 m) where near-bottom oxygen concentrations were usually lowest (often <0.1 ml/l) and organic-matter (% organic carbon and chlorophyll *a*) availability was high, (2) the coarse-grained lower summit (770–1000 m) where near-bottom oxygen concentrations were usually slightly higher (0.11 to 0.16 ml/l) and organic-matter availability remained high, (3) the coarse-grained flank (1000–2000 m) where oxygen concentration was intermediate (0.7–0.9 ml/l) and sediment organic-matter content was very low, and (4) the finer-grained base (2000–3500 m) where oxygen values exceeded 2.5 ml/l, sediment organic carbon was moderate, and chlorophyll *a* was low.

Abundances of larger forms (megafauna and macrofauna) were severely reduced on the upper summit, but attained high values (2.25/m^2 and 8,457/m^2 respectively) just tens of meters below. The smaller forms (bacteria and meiofauna) attained peak abundances on the low-oxygen upper summit, however, abundances of harpacticoid copepods were greatly reduced on the upper and lower summit, presumably due to oxygen limitation. Macrofaunal abundance and diversity patterns along the Volcano 7 oxygen/enrichment gradient resembled those typically observed along shallow-water gradients of organic pollution. Low densities of a few soft-bodied, low-oxygen tolerant species resided on the upper summit, a high-density, low-diversity assemblage inhabited the lower summit, and low-density, high-diversity assemblages occupied the flank and base sediments. The infaunal communities on Volcano 7

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[1] Department of Marine, Earth and Atmospheric Sciences, North Carolina State University, Raleigh, North Carolina, 27695-8208, U.S.A.

[2] Previously published as Cynthia L. Thomas.

[3] Graduate School of Oceanography, University of Rhode Island, Narragansett, Rhode Island, 02882-1197, U.S.A.

support the idea that OMZ boundaries are regions of enhanced biological activity. Modern faunal distributions and biogenic structures at OMZ boundaries may be useful in reconstructing oxygenation histories of ancient marine basins.

1. Introduction

Zonation of benthic invertebrate communities by physical gradients in the ocean has been observed on both hard (Lewis, 1964) and soft substrates (Arntz, 1981) for communities with both sessile (Boesch, 1977) and motile species (Morin *et al.*, 1985). Changes in infaunal community structure have been associated with continuous gradients in depth and distance from shore (Sanders *et al.*, 1965), intensity of currents (Warwick and Uncles, 1980) and wave action (Oliver *et al.*, 1980), sediment stability (Jumars and Fauchald, 1977; Morin *et al.*, 1985), substrate type (Gray, 1974; Fresi *et al.*, 1983; Weston, 1988), organic enrichment (Pearson and Rosenberg, 1978; Weston, 1990), oxygen concentration (Sanders, 1969) and salinity (Boesch, 1977). Multiple physical factors commonly interact to mold community structure. For example, gradients in current or wave intensity often lead to variable sediment texture (Oliver *et al.*, 1980), sediment stability (Morin *et al.*, 1985), and organic content (Mayer, 1989), and together these factors influence microbial productivity and infaunal composition (Aller, 1989; Levin and Thomas, 1989).

The roles of organic matter and oxygen availability in structuring macrofaunal assemblages are well studied in shallow-water systems (Pearson and Rosenberg, 1978; Weston, 1990). Steep gradients in sediment organic-matter content are often paralleled by a broad range of sediment oxygen conditions, from total anoxia to saturation (Pearson and Rosenberg, 1978). Changes in infaunal species composition, abundance, diversity and organism size are commonly observed when sediment oxygen and organic-matter content are altered significantly by anthropogenic influences.

Although there is some evidence for the importance of organic-matter/oxygen gradients in oceanic waters, (Sanders, 1969; Mullins *et al.*, 1985; Wishner *et al.*, 1990), there are few thorough studies in which physical and biological properties have been characterized adequately to infer general community-level effects. Benthic responses to organic matter inputs such as phytodetritus falls or manipulated enrichments have been examined in well-oxygenated deep-sea regions (reviewed in Gooday and Turley, 1990). The influence of oxygen depletion on deep communities has been examined mainly in enclosed basins or fjords (Rhoads and Morse, 1971). Early work on these communities has revealed altered composition and abundance patterns.

Well-developed oxygen minimum zones (OMZs), defined here as midwater regions where oxygen is <0.5 ml/l, are locations in which sharp oxygen and organic-matter gradients co-occur in the open ocean (Anderson *et al.*, 1982; Karl and Knauer, 1984). These pronounced OMZs generally develop beneath highly productive surface waters and occur in the eastern tropical Pacific, in the eastern Atlantic off NW

Africa and in the Arabian Sea (Wyrtki, 1966). Sharp oxygen interfaces also exist above anoxic basins, such as the Black Sea and the Santa Barbara Basin. Evidence exists for enhanced biological activity (both microbial and eucaryotic) near the upper and lower OMZ boundaries and at anoxic basin interfaces (Sanders, 1969; Karl and Knauer, 1984; Mullins *et al.,* 1985; Wishner *et al.,* 1990).

The work presented here examines benthic community responses to oxygen and organic-matter gradients on a seamount (Volcano 7) that intercepts the lower boundary of the eastern tropical Pacific OMZ. There is strong faunal zonation associated with the OMZ near the summit of this seamount (Wishner *et al.,* 1990). Here, we document the variable responses of different benthic size classes to physical gradients down the entire seamount. We also evaluate the importance of sediment composition and texture relative to bottom-water oxygen and sediment organic matter in determining the structure of bathyal infaunal assemblages, since seamounts often exhibit considerable heterogeneity in sediments due to topography-intensified flows, depth-associated gradients in temperature and calcium carbonate dissolution, and variable sediment sources (Levin and Nittrouer, 1987, Levin and Thomas, 1989). These findings are proposed to have implications for: (1) understanding the distribution of modern deep-sea organisms, and (2) interpreting paleoassemblages as dysaerobic (low oxygen) facies.

2. Study area and methods

Volcano 7 (13° 25′N 102° 35′W) is a conical seamount located approximately 360 km west of Acapulco, Mexico, on part of the East O'Gorman fracture zone. It has a basal diameter of 25 km and rises from a 3400 m seafloor to a summit depth of 730 m. The seamount sits on crust approximately 3.0 my old (Batiza *et al.,* 1989). The substrates available for faunal habitation are a mixture of fresh basalt, foraminiferal sands and Mn-rich fine sediments (Batiza *et al.,* 1989; Levin and Nittrouer, 1987).

The fauna of Volcano 7 was studied during two cruises with the RV *Atlantis* II and submersible *Alvin.* In June 1984, the volcano was surveyed photographically with the camera sled ANGUS and benthic samples were collected on four *Alvin* dives (Batiza *et al.,* 1989). Indications of unusually high animal abundances at the summit prompted a return cruise (12 *Alvin* dives) to study water column and benthic faunal zonation in November–December 1988 (Wishner *et al.,* 1990). Submersible dives occurred on the summit (7 dives), southwestern flank (4 dives) and southern, western and northern base regions (1, 3, and 1 dive, respectively) (Fig. 1). Sample depths ranged from 745 m to 3353 m.

Temperature, salinity and dissolved oxygen in the water column were measured with a SBE 19 Seacat CTD profiler. Dissolved oxygen concentrations were calibrated by the Winkler titration method (Carritt and Carpenter, 1966) for individual water samples from hydrocasts. The oxygen values from the CTD electrode were transformed based on a linear equation relating the two sets of measurements. Thirty-one

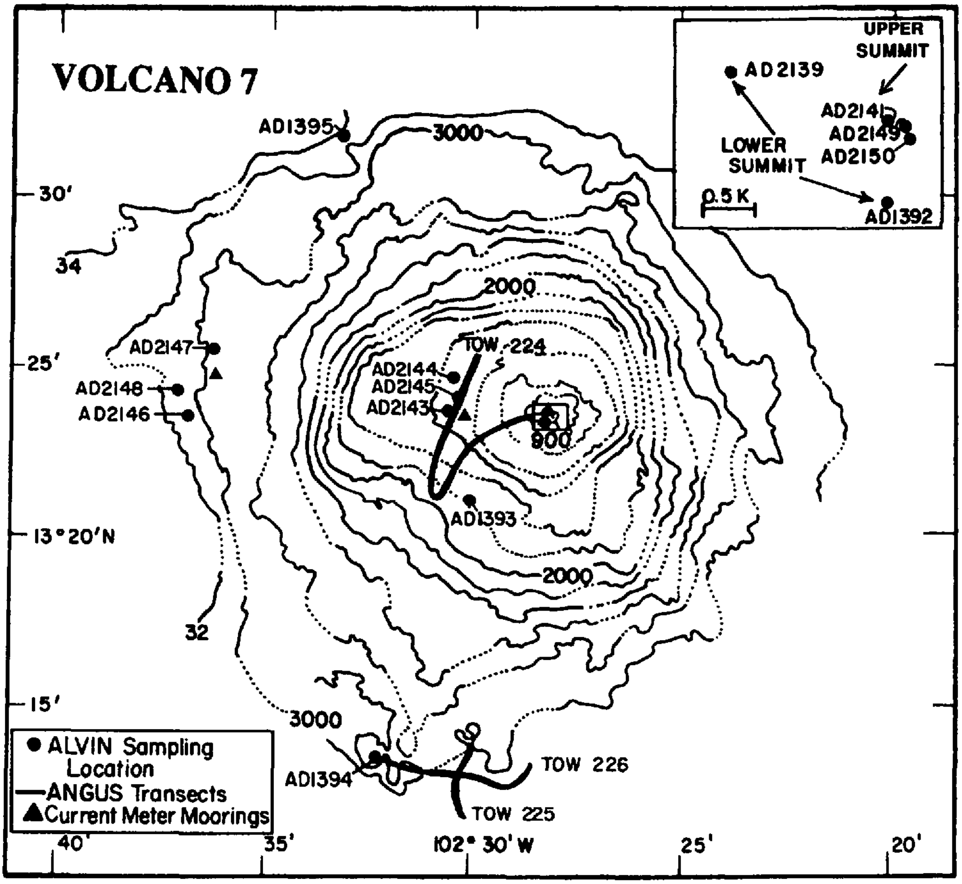

Figure 1. Location of *Alvin* dives, ANGUS camera sled tows, and current meter moorings on Volcano 7.

CTD casts were made at locations on the seamount and along north-south and east-west transects extending up to 40 km away from the summit. Salinity and temperature of bottom waters were determined with a Seacat CTD mounted on *Alvin.* Determination of oxygen concentrations in near-bottom water (within 2 m of the sea floor) was done by Winkler titration on water samples collected with a Niskin bottle mounted on the submersible.

Currents were measured in 1988 once at each of three sites: summit (800 m), flank (1290 m) and base (2979 m) (Fig. 1). Measurements were made 4.5 m above the sea floor with an Aanderaa RCM8 current meter deployed for a 3-day period sequentially at each site.

Sediments were sampled with various coring devices by *Alvin.* The spatial arrangement of sampling sites varied for each zone studied on the seamount (Fig. 1). Two box cores and one tube core were taken on most dives, usually within 5 m of each other. Sampling on the upper summit (745–767 m) took place on three dives, with sample sites covering an area less than 0.25 sq. km. Samples from the lower summit (788–857 m) were collected about 1 km away from the upper summit, with the two lower summit sampling areas less than 1 km apart on the southwest side of the seamount. Flank samples, collected on 4 dives, were from a region 2 km wide on the western flank (1316–1350 m), and an area about 4 km away on the southern flank (1790 m). Base samples (2977–3353 m) were taken during three dives on the western base, within 2 km of each other, one dive on the southern base, and one dive on the northern base. The latter two sampling areas were approximately 16 and 13 km away from the western sampling area, respectively. The numbers and types of cores collected on each *Alvin* dive for physical, chemical and biological analyses of sediments are summarized in Appendix I.

Infauna were sampled with 15 × 15 × 20 cm Ekman-style box corers containing 4 (7 × 7 × 15 cm) square subcores. On board ship, each subcore was sectioned horizontally at vertical intervals of 0–2, 2–5, 5–10 and 10–15 cm. The top two fractions were sieved through a 63-μm screen, and the bottom two through a 300-μm screen prior to preservation in 10% buffered formalin. In the laboratory, metazoan meiofauna (≥ 63 μm) were sorted from the top two fractions (0–2 and 2–5 cm) of 1 subcore per boxcore. Foraminifera were not analyzed. Macrofauna (≥ 300 μm) were sorted from all vertical fractions in all 4 subcores of each boxcore and were identified to the lowest taxonomic level possible. Meiofauna were identified to major taxon only.

Sediments for analyses of microbial abundance, textural, and organic-matter characteristics were collected in tube corers (7 cm diameter × 20 cm depth). Tube cores were taken within a few meters of the box cores and were subsampled on board ship with either acrylic tubes (2 cm diameter × 10 cm deep) for sedimentological analyses or sterile glass tubes (1.5 cm diameter × 15 cm deep) for bacterial counts. The acrylic cores were frozen immediately for later analyses of grain size, organic content, carbonate composition and chlorophyll content. The glass cores were sectioned vertically at 1-cm intervals and preserved in sterile test tubes containing 0.2-μm filtered seawater and 2.5% glutaraldehyde.

Acridine orange direct counts of bacterial abundance were made in the laboratory using the methods of Hobbie *et al.* (1977) modified for sediments (Levin and Thomas, 1989). Grain size was analyzed at 0.5 phi intervals for the top 10 cm combined using methods described in Levin and Nittrouer (1987). Twenty-five grams of bulk sediment were required to obtain sufficient particles for analysis of the fine fraction (<64 μm), thus it was necessary to process acrylic core samples down to 10 cm depth. Analyses of carbonate and organic content were carried out on homogenized samples of the upper 2 cm of sediment. Percent carbonate was determined as weight loss after 4 leachings with 10% phosphoric acid and the remaining sediment was analyzed on a Carlo Erba elemental analyzer for percent carbon and nitrogen by weight. These methods are described in greater detail in Levin and Thomas (1989).

Pigment content of sediments was determined for the upper 1 cm of each core. Pigments were extracted with acetone in the dark for 24 hrs under refrigeration; the samples were then centrifuged and the extract was frozen. This procedure was carried out three times to obtain a total extract volume of 30 ml. Chlorophyll *a* and phaeopigments were analyzed using the spectrophotometric methods of Parsons *et al.* (1984).

Abundances of megafauna were quantified from 1988 *Alvin* photographs taken with an external, hull-mounted camera, using a perspective grid to calculate surface area, and from 1984 ANGUS camera sled photographs, in which area was calculated as 1.25 sled altitude × 1.8 sled altitude. The 1984 ANGUS photographs, shot at a rate of 3 per minute, included 1491 frames (85,700 sq. m) taken during two transects totalling 23.9 km in length. Two hundred fifty-one 1988 *Alvin* photographs were analyzed, with a minimum of 771 square meters of sea floor surveyed. Total abundance data from both dates were combined for presentation here. Solitary coelenterates, which appeared in a number of the *Alvin* photographs, were excluded from the analysis because they were too small to be seen reliably in ANGUS pictures. Only metazoan megafauna are considered in the data presentation and analysis.

ANOVA assumptions of symmetry and heteroscedasticity were checked for untransformed physical, chemical and biological data by examining residual plots. When the assumptions were not met, square root, log and arcsine-transformations (in the case of proportions) were applied, residuals were examined and the best transformation was selected. As a result, microbial and harpacticoid counts, oxygen concentration, organic carbon, organic nitrogen, C:N ratios, and sediment sorting were analyzed untransformed. Percent sand, silt, and clay, as well polychaete feeding-mode representation and reproductive activity were arcsine transformed. Meiofaunal abundance was log-transformed, and megafaunal abundance, macrofaunal abundance, chlorophyll *a* and phaeopigment concentrations were square-root transformed ($\sqrt{x + 0.5}$). In all cases where necessary, transformations removed heteroscedasticity.

Physical and faunal data were analyzed for 4 depth zones: the upper summit (730–770 m), the lower summit (770–1000 m), the flank (1000–2000 m), and the base (2000–3500 m) (Fig. 2A–D). The analyses were carried out using SAS General Linear Models nested ANOVA procedure, where the model included terms for depth zone, patches within zones, and samples within patches. Comparisons of depth zones were made against an error term representing patch within zone variances, where patches were samples collected near one another on the same *Alvin* dive, or photographs taken near one another on the same *Alvin* dive or ANGUS tow. Fisher's LSD *a posteriori* test was carried out on the adjusted means (LS MEANS), also using patch within zone as the error term. Interaction between depth zone and vertical

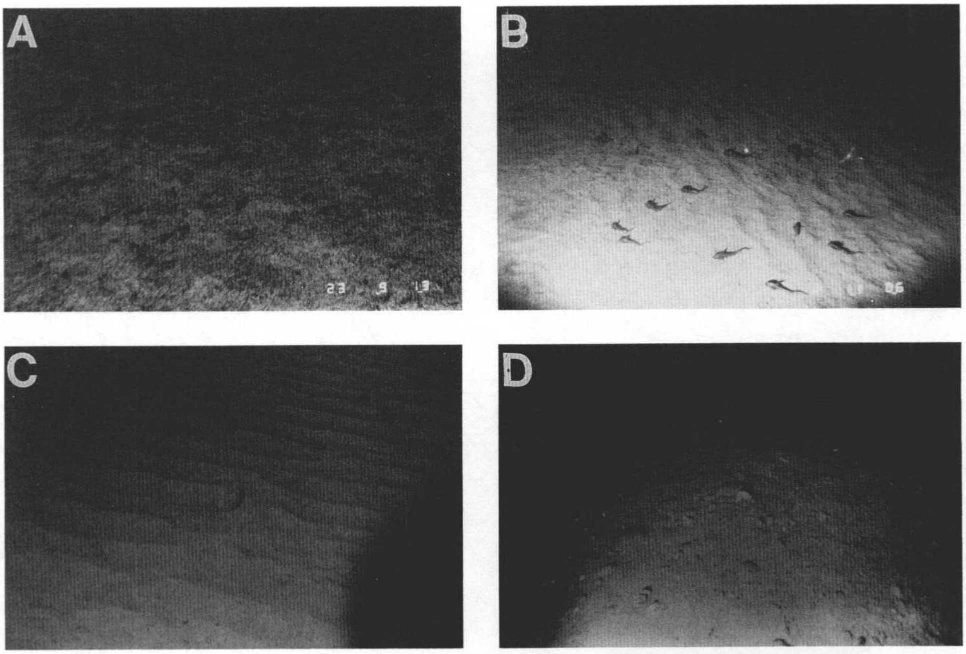

Figure 2. Photographs of the 4 zones studied on Volcano 7. (A) Upper summit, 750 m, *Alvin* Dive 2139. The fuzzy appearance of the sediment surface may indicate the presence of a microbial or protozoan mat. (B) Lower summit, 780 m, *Alvin* Dive 2149. Rattails (*Nezumia liolepis*) dominate. White specks are galatheid crabs (*Munidopsis* c.f. *hystrix*). (C) Flank, 1790 m, *Alvin* Dive 1393. A xenophyophore test (*Reticulammina* sp.) is in the center. (D) Base, 3100 m, *Alvin* Dive 2146. Protruding structures are sediment-covered rocks and xenophyophores.

distribution of macrofauna and meiofauna in sediments was analyzed using a repeated measures analysis, where depth in the sediment was the repeated measures factor, followed by pairwise comparisons of the adjusted means for data within a vertical fraction using an appropriate error term.

Rarefaction curves for diversity analyses were generated for each boxcore collected using the program PRARE1 (Sanders and Grassle, 1972).

Regression analyses were carried out using Statsview 512+ (Brainpower Inc., 1986) to examine relationships between faunal abundances (bacteria, meiofauna and macrofauna were analyzed separately) and the following physical properties: bottom-water oxygen concentration, sediment POC, PON, chlorophyll *a*, % sand, % silt, % clay and C:N ratio. Initially, simple linear regressions were performed between each measure of faunal abundance and each physical property. Those physical parameters that were significantly correlated with a given measure of faunal abundance were then added one at a time into a multiple regression model until the adjusted R^2 did not increase. Any variable in the resulting model whose coefficient had $P > 0.10$ was then deleted to produce the final model. In the case of macrofauna, multiple regressions were carried out for macrofauna deeper than 770 m (lower summit and below) only. The markedly reduced macrofaunal densities on the low-oxygen upper summit appeared indicative of some sort of threshold effect, and precluded linearity.

3. Results

a. Hydrography. A pronounced water column oxygen minimum zone exists in the Volcano 7 region (Wyrtki, 1966). From the CTD casts during the 1988 cruise, the core of the oxygen minimum ($O_2 < 0.5$ ml/l) extended from median depths of 72–1302 m and the lowest oxygen (<0.1 ml/l) from median depths of 288–1077 m (Wishner *et al.,* 1990). Thus the summit of the seamount intercepted the base of the oxygen minimum zone (Fig. 3A), and oxygen concentrations increased downslope (Fig. 3B). Oxygen in near-bottom water samples obtained by submersible was 0.08–0.09 ml/l on the upper summit (733–746 m), 0.11–0.16 ml/l on the lower summit (806–815 m), 0.70–0.86 ml/l on the flank (1308–1343 m), and 2.52–2.57 ml/l at the base (2978–3150 m) (Fig. 3B, $r^2 = 0.994, p < 0.01$ for linear regression of submersible oxygen samples with depth).

The CTD data, however, suggested a more dynamic and complicated situation, especially at the summit. In 6 of 7 CTD casts taken above the seamount, oxygen was lower at 730 m than at 800 m (mean difference = 0.011 ± 0.014 ml/l), but the concentration ranges measured at these two depths substantially overlapped. Sensor drift and the resolution limits of both the sensor and the Winkler calibrations contributed to the difficulty of determining the magnitude and variability of this small difference. In addition, temperatures obtained in conjunction with current velocities at the summit showed diurnal and semidiurnal fluctuations of 0.5°C, indicating tidal displacement of water masses passing over the seamount (L. Mullineaux, pers. comm.). Thus, although the upper summit at a given time may experience slightly lower oxygen concentrations than the lower summit, the oxygen environment at any particular summit location is most likely one of periodic variation, rather than a constant concentration and simple depth gradient (Wishner *et al.,* 1990).

b. Currents. During the 1988 cruise, the strongest flows occurred on the flank, where the median current velocity was 8.1 cm/sec and the peak velocity 17.7 cm/sec. About 23% of the records on the flank indicated velocities below detectable levels for these current meters (<2 cm/sec), and 29% of the time velocities were >10 cm/sec (Fig. 4). Currents were slower on the summit, with 90% of the values <6.9 cm/sec (60% below detectable limits) and only 0.7% $>$ 10 cm/sec (peak = 15.3 cm/sec). The base was the most quiescent location, with 83% of the records below detectable limits and a peak velocity of only 8.9 cm/sec (Fig. 4). Diurnal and semidiurnal tidal periodicity was evident in a 10-day record from the summit (L. Mullineaux, pers. comm.).

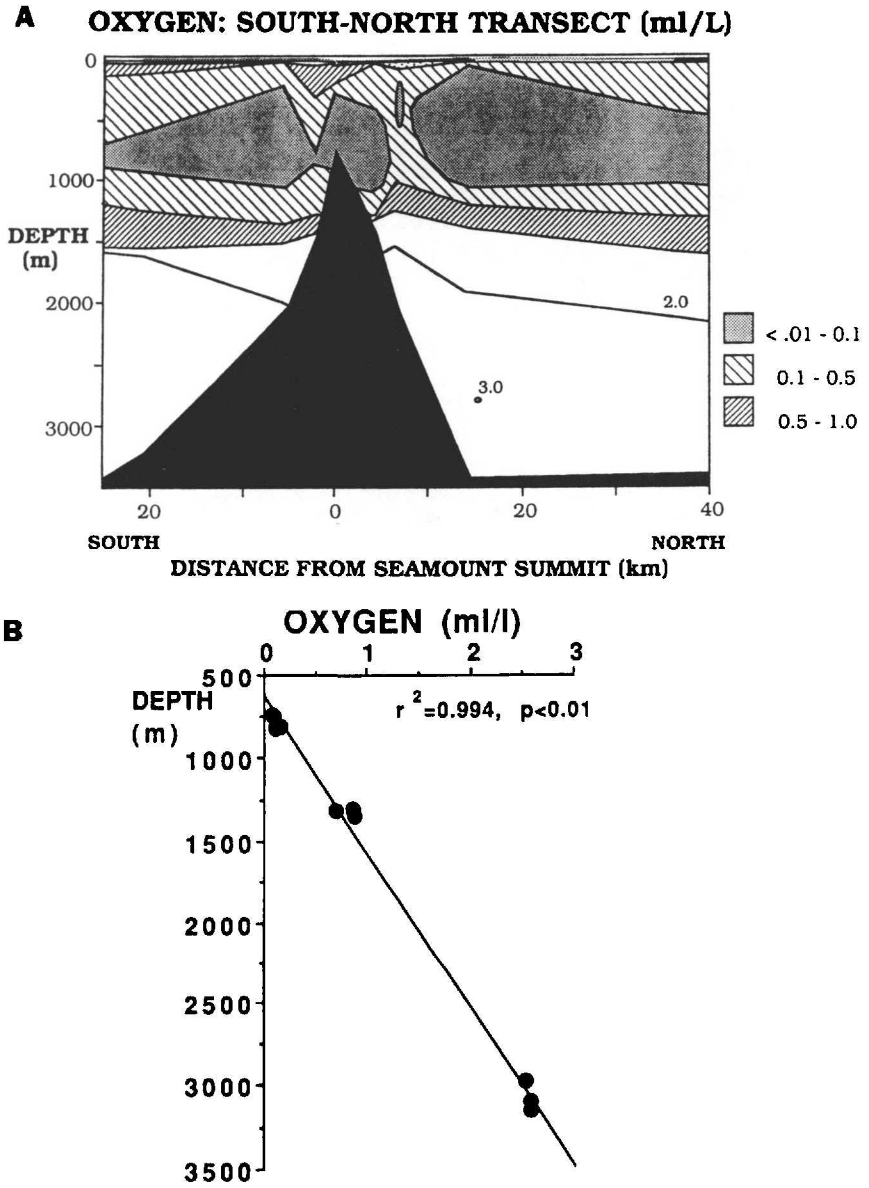

Figure 3. (A) Oxygen concentration in the water column along a south-north transect over the seamount. Data are from 10 CTD profiles taken between Nov. 26–Dec. 3, 1988. (B) Near-bottom (< 2 mab) oxygen concentrations in water samples taken along the western slope of Volcano 7. Water was collected in Niskin bottles attached to *Alvin*.

c. Sediments. Sediments of the upper and lower summit as well as the flank were dominated by foraminiferal sands (78%, 81%, and 75% sand, respectively) (Table 1, Figs. 2A–C). During both cruises the summit sands were olive green in color and the flank sands were tan. The base region (Fig. 2D), located below the lysocline (which is

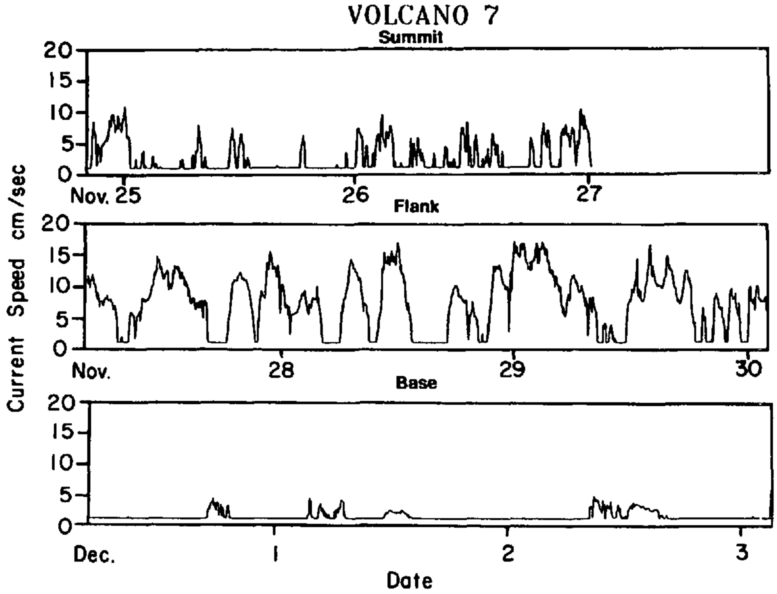

Figure 4. Three-day current measurements made in Nov.–Dec. 1988 4.5 m above the bottom with an Aanderaa RCM8 current meter. (A) Summit (800 m); (B) Flank (1290 m); (C) Base (2979 m).

about 2500 m in this area), contained little sand (13%) and the soupy, dark-brown, Mn-rich surface sediments (dissociated for analysis) were largely (51%) clay-sized particles. Calcium carbonate content of sediments was highest on the flank (91%), moderately high at the upper (81%) and lower (80%) summit, and low at the base (15%) (Table 1). Sediment percent organic carbon (POC) and percent organic nitrogen (PON) contents were 3.35% and 0.46%, respectively on the upper summit and approximately 60% lower on the lower summit. The upper summit values were much higher than we expected for coarse-grained sediments in an open-ocean setting, and were significantly higher than the lower summit, flank and base values (Table 1). Most of the sediments from the summit and base exhibited C:N between 7 and 9 (Table 1), indicating the presence of relatively fresh organic material (Banse, 1974). C:N values did not vary significantly with depth.

Like organic carbon and nitrogen, chlorophyll *a* and phaeopigment content of sediments was unusually high at the summit (Table 1). Pigment concentrations were similar at the upper and lower summit, in contrast to the decrease observed in POC and PON (Table 1). Summit pigment values were an order of magnitude higher than flank and base values.

Physical differences among the Volcano 7 depth zones are summarized as follows. The upper and lower summit were statistically indistinguishable from one another with respect to sediment grain size, carbonate and plant pigment content. Although

Table 1. Physical properties of bottom water and sediments on Volcano 7. Entries with similar letters are not significantly different from one another. The oxygen values are from the *Alvin*-collected water samples.

	Upper Summit (745–767 m)		Lower Summit (788–857 m)		Flank (1316–1790 m)		Base (2798–3353 m)		ANOVA*		
	$\bar{x}$ ± 1S.E.	*n*	$\bar{x}$ ± 1S.E.	*n*	$\bar{x}$ ± 1S.E.	*n*	$\bar{x}$ ± 1S.E.	*n*	*df*	*F*	*P*
Bottom Water Oxygen (ml/l)	0.09^a ± 0.01	2	0.13^a ± 0.03	3	0.81^b ± 0.10	3	2.55^c ± 0.03	3	3,7	1165.2	<0.0001
Sediment Grain Size											
Percent Sand	77.95^a ± 2.65	4	81.17^a ± 4.34	4	74.90^a ± 2.04	3	13.12^b ± 8.11	6	3,12	69.4	<0.0001
Percent Silt	8.15^a ± 2.06	4	$10.75^{a,b}$ ± 4.31	4	18.28^b ± 4.05	3	36.09^c ± 4.40	6	3,12	33.5	<0.0001
Percent Clay	13.90^a ± 3.21	4	8.08^a ± 3.19	4	6.81^a ± 6.06	3	50.80^b ± 10.52	6	3,12	36.6	<0.0001
Sorting (phi)	3.11 ± 0.27	4	2.58 ± 0.38	4	2.07 ± 0.48	3	2.73 ± 0.54	6	3,12	35.0	NS
Sediment Content											
Percent $CaCO_3$	81.29^a ± 1.12	3	80.24^a ± 2.72	4	91.22^b ± 2.78	4	14.69^c ± 10.00	3	3,10	157.5	<0.0001
Percent Organic C	3.35^a ± 0.58	3	1.48^b ± 0.72	4	0.56^c ± 0.33	4	$1.17^{b,c}$ ± 0.23	3	3,11	18.9	<0.0001
Percent Organic N	0.46^a ± 0.09	3	0.18^b ± 0.10	4	0.06^c ± 0.05	4	0.16^b ± 0.02	3	3,11	18.9	<0.0001
C:N Ratio (weight)	7.33 ± 0.14	3	8.52 ± 0.83	4	11.89 ± 5.50	3	7.54 ± 1.00	3	3,11	1.9	NS
Chlorophyll *a* (μg/g)	15.31^a ± 14.53	2	15.63^a ± 8.02	3	0.73^b ± 0.53	4	1.24^b ± 1.75	3	3,8	8.4	0.0076
Phaeopigment (μg/g)	15.10^a ± 9.83	2	23.75^a ± 6.31	3	1.75^b ± 0.64	4	2.02^b ± 2.69	3	3,8	20.9	0.0004

*Depth zone effects were tested against patch within zone variance.

Alvin-based measurements of bottom-water oxygen concentration were all lower on the upper summit than the lower summit, sample size was too small to distinguish the two zones statistically. Only POC and PON content were significantly higher on the upper than lower summit (Table 1). The flank resembled the summit sites in C:N ratio and grain size, but differed in all other physical parameters examined, having more calcium carbonate and oxygen but less POC, PON, chlorophyll *a*, and phaeopigment. The base differed from all other sites, having higher bottom-water oxygen concentration, finer grain size, and lower percent carbonate. The flank and base sites were similar in sediment chlorophyll *a* and phaeopigment concentrations, while the base resembled the lower summit in POC and PON content (Table 1). This is the rather complicated backdrop against which we evaluate distributions of benthic bacteria and metazoans on Volcano 7.

d. Sediment bacteria. Microbial abundances on Volcano 7 ranged from 2.21 to 7.37 × 10^8/ml in surface sediments (0–1 cm), and declined quickly with depth in the sediment to fairly uniform values (1–2 × 10^8/ml) from 5 to 15 cm (Fig. 5). In the 0–1 cm fraction, the highest counts ($\bar{x} \pm 1$ S.D.) were obtained from the upper summit (6.61 ± 0.89 × 10^8/ml) and the base (5.86 ± 0.34 × 10^8/ml). Significantly reduced counts were obtained from the lower summit (4.86 ± 0.18 × 10^8/ml) and the flank (3.43 ± 0.82 × 10^8/ml) ($F_{[3,6]} = 9.24$ $P = 0.0115$) (Fig. 6A). Bacterial abundance increased with increasing sediment percent organic carbon (3rd order polynomial, $r^2 = 0.72$, $P < 0.01$, Fig. 7A) and percent organic nitrogen (3rd order polynomial, $r^2 = 0.73$, $P < 0.01$, Fig. 7B) on most of the seamount, but decreased at the highest organic-matter and lowest oxygen levels on the upper summit.

Variance in total microbial counts was well described through multiple regression (adjusted $R^2 = 0.91$) by 4 physical properties: % clay, chlorophyll *a*, % organic N, and % organic C (Table 2).

e. Meiofauna. Over 98% of the meiofauna collected on Volcano 7 were nematodes and harpacticoid copepods (Fig. 8). Ostracods, polychaetes, kinorhynchs, nemerteans, aplacophorans, bivalves, loriciferans, tardigrades, an amphipod and a gastropod were also present in the meiofaunal size fraction. Metazoan meiofaunal densities ($\bar{x} \pm 1$ S.D.; upper 5 cm only) were highest on the upper summit (194 ± 89 × $10^3/\text{m}^2$), and 2–8 times lower on the lower summit, flank and base (26–93 × $10^3/\text{m}^2$) ($F_{[3,6]} = 49.21$, $P < 0.0001$, Fig. 6B). Sediment chlorophyll *a* concentration could account for 39% of the variance in total meiofaunal densities ($P = 0.0028$, Table 2), but no other physical parameters produced a significant regression coefficient.

Harpacticoid copepods exhibited downslope abundance patterns different from those of total meiofauna (Fig. 6B). Harpacticoid copepods were extremely rare on the upper summit ($\bar{x} \pm 1$ S.D./core = 4.2 ± 1.9), increased in abundance on the lower summit (24.5 ± 5.0), and exhibited greatest densities on the flank (173.2 ± 37.1)

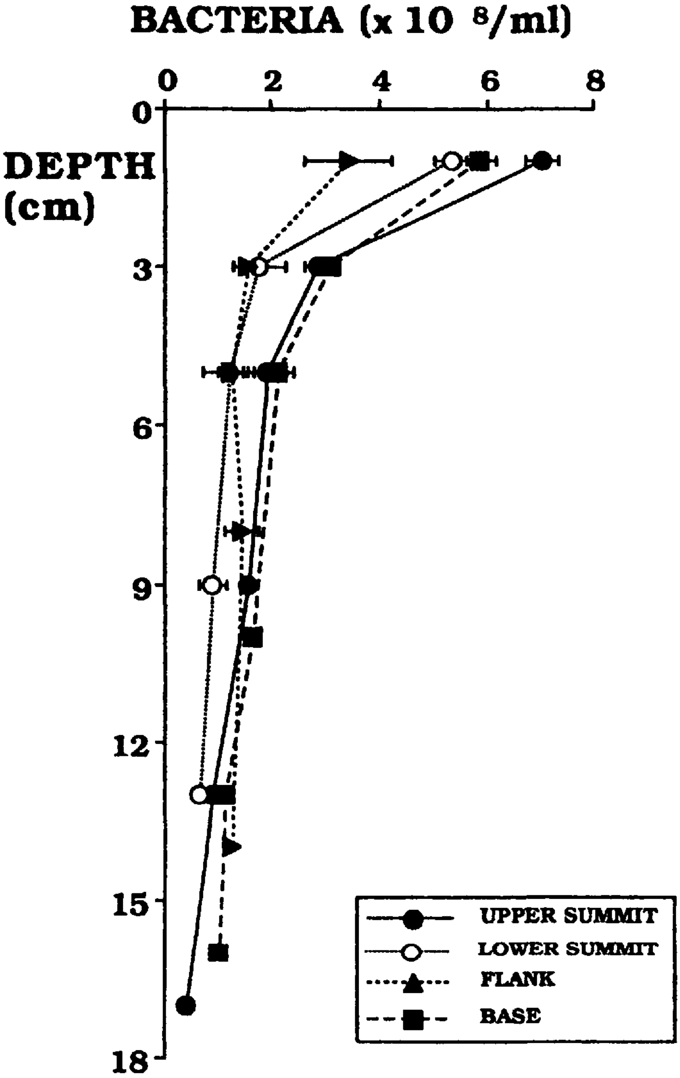

Figure 5. Vertical distribution of (acridine orange direct) bacterial counts in Volcano 7 sediments at upper summit (746–766 m), lower summit (807–857 m), flank (1320–1350 m) and base (2977–3118 m) sites.

and base (103.7 ± 28.5) ($F_{[3,6]} = 56.25$; $P < 0.0001$). Thus, the relative contribution of harpacticoid copepods to total meiofauna increased downslope (Fig. 8), while the ratio of nematodes to harpacticoid copepods in each core decreased downslope from mean values of 252 (range = 115–546) on the upper summit, to 4.0 (range = 2.8–5.2) on the lower summit, 1.5 (range = 1.3–1.8) on the flank, and 1.8 (range = 1.4–2.0) at the base.

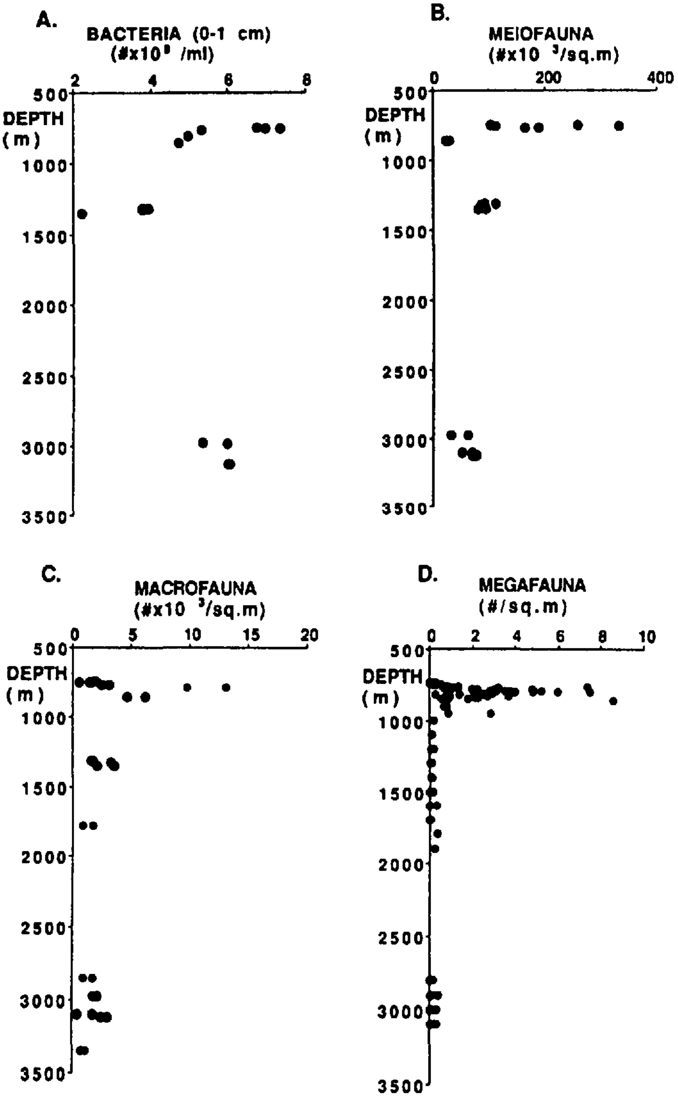

Figure 6. Total abundances of (A) Bacteria, (B) Meiofauna, (C) Macrofauna, and (D) Megafauna as a function of depth. Data points are counts from individual cores.

Vertical distribution of meiofauna within sediments varied among depth zones ($F_{[3,7]} = 9.21$; $P = 0.0079$). Meiofauna were heavily concentrated in the surface fraction (0–2 cm) on the flank (86.6% of total meiofauna residing in the upper 2 cm) and upper summit (80.4%) and significantly less so on the lower summit (63.4%) and base (64.7%) (Fig. 8).

f. Macrofauna. In contrast to the meiofauna, which attained maximum densities on the upper summit, average macrofaunal densities ($\bar{x} \pm 1$ S.D.) were approximately 4

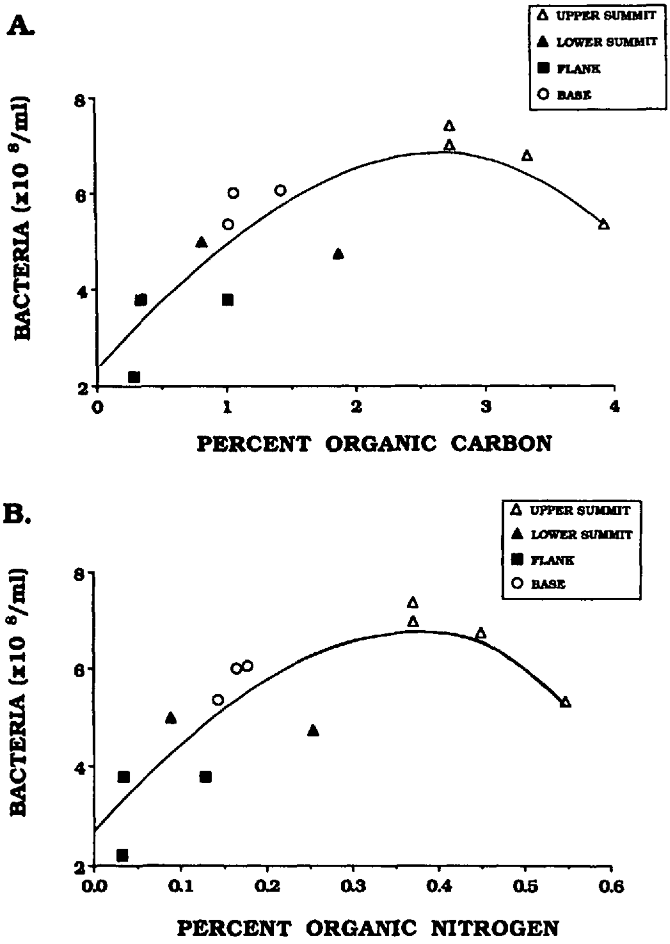

Figure 7. Third order polynomial regression of sediment bacteria on organic matter content. (A) Sediment bacteria on percent organic carbon, $r^2 = 0.722$, $P = <0.01$. (B) Sediment bacteria on percent organic nitrogen, $r^2 = 0.734$, $P = <0.01$.

times higher on the lower summit (8,457 ± 3,769/m^2) than in the other three zones (Fig. 6C) ($F_{[3,10]} = 10.39$; $P = 0.0020$). Average macrofaunal densities on the upper summit (1,854 ± 877/m^2), flank (2,165 ± 948/m^2) and base (1,612 ± 801/m^2) did not differ significantly from one another (Fig. 6C). Of the physical parameters examined by regression, chlorophyll *a* concentration in sediments and bottom-water oxygen concentration could explain 91% of the variance in abundance of macrofauna collected deeper than 770 m ($P < 0.0001$; Table 2).

Differences in macrofaunal species composition were observed among depth zones (Fig. 9, Appendix II). The upper summit zone was dominated (47.3% of individuals) by an unidentified aplacophoran species (family Lepidomeniidae), the

Table 2. Regression models of faunal abundance and physical properties on Volcano 7. The *P* values represent the significance of independent variables in the final model.

A. BACTERIA

$F_{4,9} = 33.347$ $P < 0.0001$ Adjusted $R^2 = 0.91$

Parameter	*Coefficient*	*P*
Intercept	2.936	
Percent Clay	4.426	<0.0001
Chlorophyll *a*	0.091	0.0002
Percent Organic N	1669.85	0.0354
Percent Organic C	−189.335	0.0791

B. MEIOFAUNA

$F_{1,17} = 12.14$ $P = 0.0028$ Adjusted $R^2 = 0.38$

Parameter	*Coefficient*	*P*
Intercept	68.265	
Chlorophyll *a*	5.106	0.0028

C. MACROFAUNA (>770 m)

$F_{2,18} = 489.474$ $P < 0.0001$ Adjusted $R^2 = 0.90$

Parameter	*Coefficient*	*P*
Intercept	2.363	
Chlorophyll *a*	0.501	<0.0001
Oxygen	−0.566	.0372

paraonid polychaete *Cirrophorus lyra* (17.9%), the dorvilleid polychaete *Protodorvillea* sp. A (7.8%) and unidentified pogonophorans (6.0%). Polychaetes comprised only 33.0% of the total macrofauna. At the shallowest sites sampled (745 m), only one polychaete species (*Protodorvillea* sp. A), chaetognaths, an unidentified pogonophoran, Lepidomeniomorph aplacophorans and a single ophiuroid were present. Other polychaete species present in upper summit sediments included a hesionid, (*Bonuania* sp.), two cirratulids, (*Tharyx* sp. A and a single specimen of *Caulleriella* sp. 2), and a flabelligerid, (*Flabelliderma* sp.). Peracarid crustaceans and coelenterates were conspicuously absent from upper summit sediments, and molluscs other than aplacophorans were rare.

Just tens of meters deeper, on the lower summit, species composition was dominated by polychaetes (70.8%; Fig. 9). Although 19 polychaete species were present in this zone (Appendix II), most individuals (85.5%) belonged to the species *Tharyx* sp. A, *Euchone incolor, Cirrophorus lyra, Protodorvillea* sp. A, and *Caulleriella* sp. 1. All of the 6 polychaete species present on the upper summit were also collected on the lower summit except for *Caulleriella* sp. 2. The other dominant taxon present in the lower summit region was an unidentified species of burrowing anemone, which comprised 21.3% of the total macrofauna. This species of anemone was common in 1984 on the lower summit, but in 1988 was found only on the flank. The Lepidomeniomorph aplacophoran, which comprised nearly half of all individuals on the upper summit, was rare on the lower summit (0.3%). An unidentified bivalve species

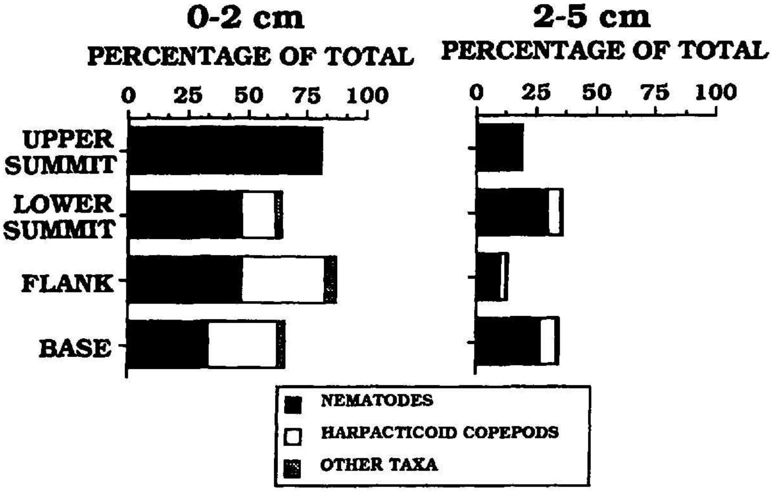

Figure 8. Distribution of major meiofaunal taxa (≥ 63 µm) in upper summit (745–767 m), lower summit (857 m), flank (1320–1350 m) and base (2978–3118 m) sediments on Volcano 7. Two sediment depth zones (0–2 cm and 2–5 cm) are shown.

comprised 3–4% of the total macrofauna on both the upper and lower summit. No peracarid crustaceans were collected on the lower summit.

The flank and base settings shared 35 species in common (41–44% of the total numbers recorded at the two sites) (Appendix II). Polychaetes comprised 62.0% and

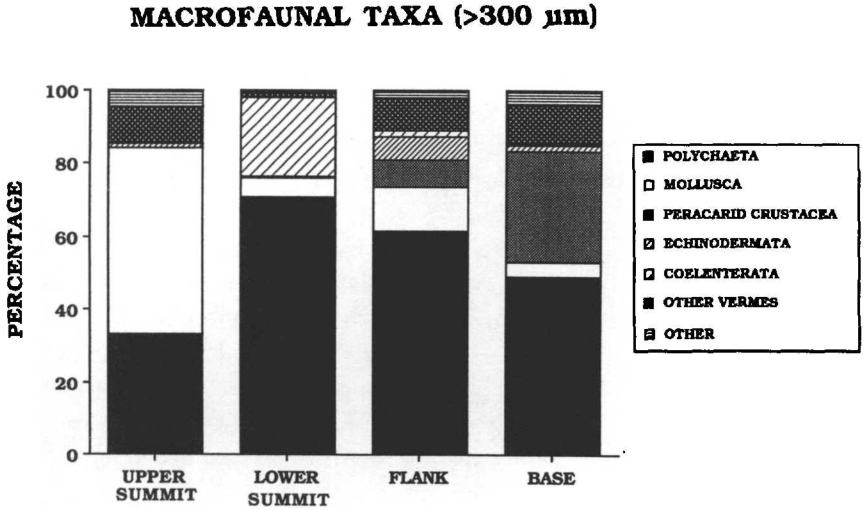

Figure 9. Major taxon composition of macrofauna (≥ 300 µm) in upper summit (745–767 m), lower summit (788–857 m), flank (1320–1790 m) and base (2850–3353 m) sediments on Volcano 7.

49.5% of the total macrofauna on the flank and base, respectively. Molluscs were more common on the flank (12%) than base (3%), whereas peracarid crustaceans were more common at the base (31%) than on the flank (7%). The most abundant species on the flank was a polychaete, *Fabrisabella similis* (4.7% of the total). The most abundant species at the base was a tanaid, *Filitanais* sp. GG (8.3% of the total).

Vertical distribution of macrofauna in sediments varied by depth zone ($F_{[9,21]} = 4.90$, $P = 0.0013$), with the flank fauna generally shifted upward in the sediments relative to the distributions at other sites. The 0–2 cm fraction contained the majority of macrofauna at all sites, but a significantly greater proportion of total individuals were found in the surface fraction on the flank (mean of 76%) than on the upper summit (62%), lower summit (66%), or base (55%).

Macrofaunal species richness was lowest on the upper summit (14 spp. among 218 individuals), over twice as high on the lower summit (32 spp. among 663 individuals), and considerably higher on the flank (81 spp. among 297 individuals) and base (86 spp. among 316 individuals). The species counts for macrofauna are minima because of the occurrence of unidentified species in some taxa. A cumulative percent curve by species rank shows strong dominance by a few species on the upper and lower summit and considerably less dominance at the flank and base sites (Fig. 10A). Rarefaction curves of expected macrofauna species numbers show lowest species diversity at the upper summit, slightly increased diversity at the lower summit and highest diversity on the flank and base (Fig. 10B).

Feeding patterns of polychaetes (which comprised 59% of the total macrofauna) were inferred from morphology and the literature (sensu Fauchald and Jumars, 1979; Maurer and Williams, 1988). Carnivory and scavenging representation was greatest on the uppermost summit (63.5% of all individuals), but not significantly different from the base (37.0%) ($F_{[3,11]} = 2.97$, $P = 0.0784$). Surface-feeding modes (suspension and surface-deposit feeding) were rarely observed on the uppermost summit, relative to the other sites ($F_{[3,11]} = 5.989$, $P = 0.0120$), while the proportion of subsurface feeders was similar at all sites (14–29%) ($F_{[3,11]} = 0.21$ $P = 0.8863$) (Fig. 11).

Reproductive activity at the time of sampling, recorded as the presence of maturing eggs within the body wall, or brooded embryos and larvae, was noted for polychaetes collected in 1988. Reproductive activity was most frequent for upper summit polychaetes ($\bar{x} \pm 1$ S.D. = 63.4% ± 29.8%), common for lower summit polychaetes (25.3% ± 13.1%), and rare on the flank (5.1% ± 4.2%) and base (2.2% ± 3.4%) ($F_{[3,7]} = 6.39$, $P = .0205$). The percent of polychaetes reproducing on the upper summit was significantly higher than on the flank and base, but not significantly different from the lower summit.

g. Megafauna. Abundances of epibenthic and benthopelagic metazoan megafauna, defined as those animals identifiable in bottom photographs (e.g., Grassle *et al.*, 1975;

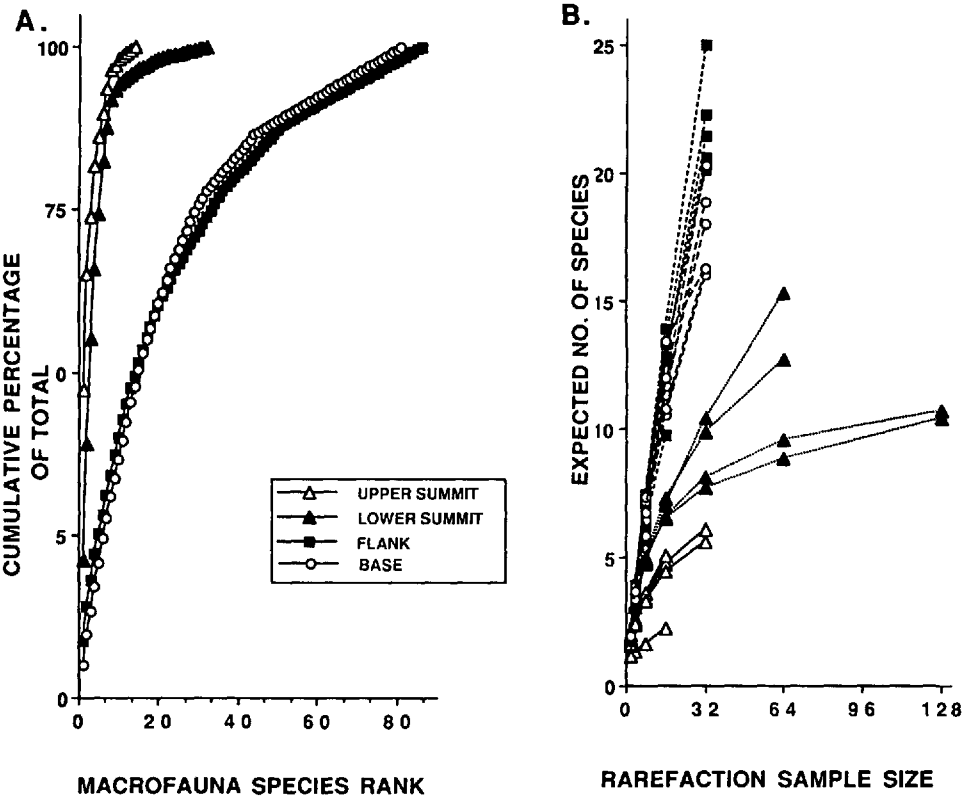

Figure 10. Diversity of macrobenthos (≥ 300 μm) in upper summit (745–767 m), lower summit (788–857 m), flank (1320–1790 m) and base (2850–3353 m) sediments on Volcano 7. Terebellid polychaete species, unidentified specimens of Sipuncula, Mollusca, Amphipoda, Anthozoa, Bryozoa, Chaetognatha, Hydrozoa, and Porifera were excluded because of lack of positive species identifications. The total number of individuals excluded was 226, representing 15.1% of the total collection. (A) Cumulative species curves indicating dominance. (B) Rarefaction curves for each boxcore taken, indicating expected species richness as a function of sample size.

Smith and Hamilton, 1983), exhibited a pattern similar to that of macrofauna (Fig. 6D). Mean abundance (±1 S.D.) was low on the upper summit ($0.74 \pm 0.65/\text{m}^2$), highest on the lower summit ($2.25 \pm 0.03/\text{m}^2$), and lowest at the flank ($0.64 \pm 0.96/\text{m}^2$) and base ($0.45 \pm 0.29/\text{m}^2$) ($F_{[3,14]} = 46.83$, $P < 0.0001$). Differences in density between depth zones were statistically significant in all comparisons except the flank and base. Upper summit (< 770 m) megafauna were comprised primarily of rattails (*Nezumia liolepis*) (49.2% of individuals) and solitary coelenterates. Rattails, anemones, galatheid crabs, serpulid polychaetes, sponges and ophiuroids dominated the lower summit. Xenophyophores (agglutinating protozoans) which were not included in the metazoan counts presented above, comprised 65.3% and 73.8% of

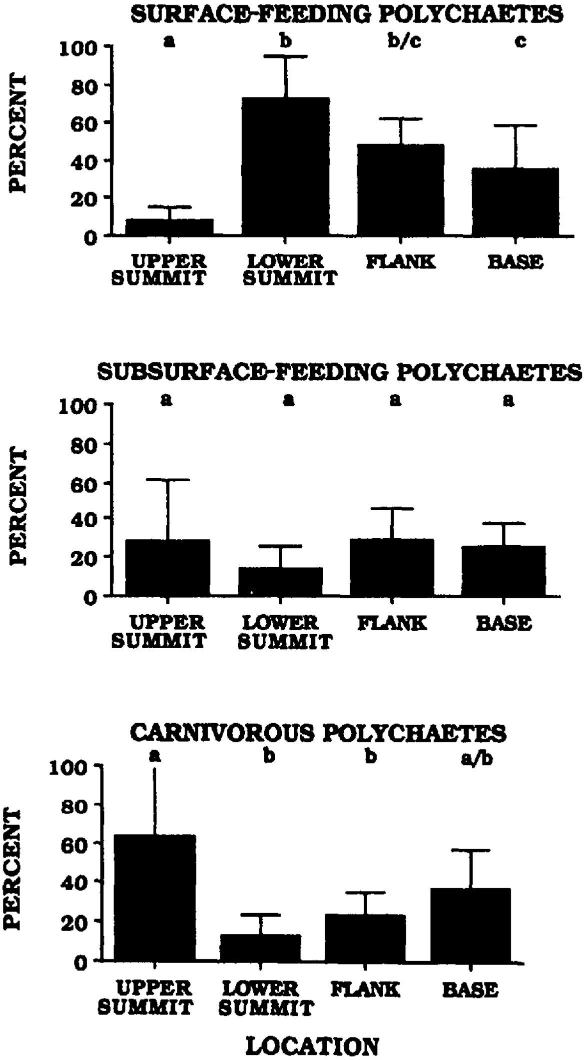

Figure 11. Representation of polychaete feeding modes (mean ± 1 S.D.) in upper summit (745–767 m), lower summit (788–857 m), flank (1320–1790 m) and base (2850–3353 m) sediments on Volcano 7. Values for zones sharing the same letter were not significantly different.

the total organisms visible in photographs on the flank and base, respectively. A detailed discussion of the xenophyophores on Volcano 7 can be found in Levin and Thomas (1988).

4. Discussion

a. Physical settings. Sediment texture and composition suggested that the seamount summit has received high fluxes of relatively fresh organic material. Visual observations of green floc on hard and soft substrates on the Volcano 7 summit indicated that phytodetritus was present in both 1984 and 1988. Preliminary radiochemical investigations also provided evidence for high particulate fluxes. Least squares fit of a single profile of excess ^{210}Pb activity in upper summit sediments (767 m) led to an "apparent accumulation rate" of 0.79 mm/yr (Levin, unpublished data). This value was taken to be a maximum rate, however, due to unresolved effects of bioturbation. It has been hypothesized that relatively undegraded organic material from surface waters reaches the seafloor here because decomposition and planktonic utilization of particulates is reduced in the sparsely-populated OMZ above Volcano 7 (Wishner *et al.*, 1990).

Sediments on the flank, where the strongest and most persistent currents were measured (Fig. 4), exhibited low values of organic matter and chlorophyll *a* (Table 1). We hypothesize that much of the low-density, organic-rich material reaching the flanks of Volcano 7 is winnowed from the surface by fast currents and deposited around the base of the seamount, where currents were slow, sediments were finer grained, and concentrations of organic matter and chlorophyll *a* were higher (Table 1). The high inventory (109.28 ± 1.02 dpm/cm^2) and deep penetration ($>$23 cm) of excess ^{210}Pb observed in a single base core (2978 m) (Levin, unpublished data) are indicative of either intense mixing or unusually high accumulation rates, relative to the summit, and to other settings at 3000 m (D. DeMaster, pers. comm.).

b. Physical control of community structure. Though separated by only tens of meters, the upper and lower summit zones had different biological assemblages, which we hypothesize is partly a size-related response to low oxygen. The smaller taxa (bacteria and meiofauna) were significantly more abundant on the upper than lower summit, while the larger taxa (macrofauna and megafauna) showed the reverse pattern (Fig. 6). We attribute this variation primarily to differential tolerance to low oxygen, which could be associated with surface to volume ratios, or with increased metabolic flexibility conferring ability to utilize food resources in the absence of oxygen (Zehnder, 1988). Greater sensitivity to hypoxia of macrofauna compared to meiofauna has been reported previously at intertidal and shelf depths (Van Es *et al.*, 1980; Josefson and Widbom, 1988), but to our knowledge, the Volcano 7 study is the first to compare responses of deep-sea organisms spanning four orders of magnitude in size (bacteria through megafauna). At the shallowest site sampled (745 m), the presence of forms reportedly tolerant to low O_2, such as pogonophorans (Southwood and Southwood, 1988), *Protodorvillea* spp. (Pearson and Rosenberg, 1978; Levin and Smith, 1984), and anemones (Jorgenson, 1980), and the absence of forms unable to tolerate low oxygen, such as harpacticoid copepods (Hicks and Coull, 1983; Murrell and Fleeger, 1989) and peracarid crustaceans, provides additional circumstantial evidence for the existence of oxygen limitation on the upper summit.

High microbial counts were associated with high sediment organic content and fine sediments (Table 2). Although counts do not reflect microbial activity levels (Jannasch and Taylor, 1984), they provide baseline information about the potential importance of bacteria at each site. Also, microbes may affect, as well as be influenced by, sediment properties such as PON or C:N ratios. The regression results for bacteria on Volcano 7 (Table 2, Fig. 7) mirror associations among bacteria, organic matter and clay content that are well documented in shallow water sediments (Mayer, 1989).

Studies of shallow systems have shown that meiofaunal abundance, composition, and diversity are strongly influenced by oxygen (Murrell and Fleeger, 1989), organic matter availability (Hockin, 1983; Sandulli and Giudici, 1989), and particle size (Hicks and Coull, 1983; Raffaelli and Mason, 1981). The substantial decrease in meiofaunal abundances between upper and lower summit sites may be the result of diminished food supply (Table 1), or increased biological interactions (competition, predation or disturbance) involving the abundant macrofauna and megafauna on the lower summit (Fig. 6).

Oxygen apparently plays little direct roll in determining total meiofaunal abundance on Volcano 7. However, the paucity of harpacticoid copepods on the upper summit probably reflects the greater sensitivity of this group to severe oxygen depletion (Coull and Chandler, 1992, Coull, personal communication). Intolerance to low oxygen among harpacticoid copepods may result from their higher metabolic requirements relative to other meiofauna, and thus diminished ability to obtain sufficient energy from anaerobic metabolic pathways (Powell, 1989; Powell, personal communication).

Although we were unable to consider meiofaunal diversity in this study, Nienstadt and Arnold (1988) did so for the benthic foraminiferal component of the meiofauna from lower summit, flank and base regions of Volcano 7 (sampled in 1984) and three other nearby seamounts. They reported unusually low diversity of benthic foraminifera between 788 and 1058 m, where a single species indicative of low oxygen conditions comprised 50–61% of the assemblage. Very high abundances and community dominance by rotaliid forms (characteristic of low-oxygen settings) were reported from 788 m on Volcano 7.

Low oxygen concentration is a likely explanation for reduced macrofaunal densities on the upper summit. The sharp increase in macrofaunal densities on the lower summit (Fig. 6C), suggests the existence of some sort of fluctuating threshold, above which oxygen availability is sufficient enough of the time to permit development of dense infaunal assemblages. Below the upper summit, both labile organic matter (chlorophyll *a*) and oxygen concentration appear to be good predictors of macrofaunal abundance (Table 2).

The relative insignificance of current regime and grain size to macrofaunal community structure is suggested by the provocative similarity of flank and base assemblages. The flank represents a high-energy, coarse-sand setting at 1200–1800 m

(Fig. 2C). In contrast, the base is a quiet, fine-grained habitat at twice the water depth (Fig. 2D). Yet macrofauna exhibited similar patterns of species dominance and richness (Fig. 10A, B), polychaete communities at the two sites shared many species (Appendix II), and polychaete feeding-mode representation (Fig. 11) and reproductive activity were nearly identical. Patterns of macrofaunal community structure on the flank and base were characteristic of many other deep sea regions (Jumars and Gallagher, 1982).

Control of deep-water infaunal community structure by oxygen has been proposed previously in regions of intense upwelling or in basins where oxygen gradients are well developed. Macrofaunal zonation patterns associated with oxygen gradients were reported by Sanders (1969) for Walvis Bay, by Rhoads and Morse (1971) for the Black Sea, Gulf of California, and southern California basins, by Thompson *et al.* (1985) for the central California slope, and are summarized by Thiel (1978) for regions off Chile and Peru. The Walvis Bay transect in SW Africa (100–450 m) exhibited diversity and density patterns along an oxygen gradient nearly identical to those observed on Volcano 7 (Sanders, 1969).

The importance of oxygen is also evident when temporal shifts in oxygen concentration generate major variations in subtidal macrobenthic communities. El Nino events, which lead to elevated oxygen concentrations in Peruvian waters, produce increases in macrobenthic density, biomass and diversity (Tarazona *et al.,* 1988a,b). Summer hypoxia, which is typical in many shallow, enclosed bays, generally leads to seasonally-reduced abundances and diversity (Van Es, 1980; Friligos and Zenetos, 1988).

c. *Oxygen minimum zone edge effects.*

Observations of high macro- and megafaunal abundances at depths between 770 and 850 m on Volcano 7 appear to be a manifestation of "edge effects" associated with the eastern Pacific OMZ. Mullins *et al.* (1985) reported increased biogeochemical activity along the edges of the central California OMZ. Abundances of macrofaunal groups and benthic foraminiferans were greatest on the upper (500 m) and lower (1000 m) edges of the central California OMZ (Mullins *et al.,* 1985; Thompson *et al.,* 1985). Peak values of calcium carbonate, glauconite and fecal pellets were all observed at upper or lower edges of the OMZ. These edge effects were attributed to the interaction of dissolved oxygen concentrations, bottom currents, food availability and bacterially-mediated nutrient recycling (Mullins *et al.,* 1985).

Karl and Knauer (1984) and Karl *et al.* (1984) noted increases in organic C and N flux at the lower edge of the eastern Pacific OMZ (700–900 m), the same depth range as the maximum Volcano 7 faunal abundances (Fig. 6). They suggested the source of these fluxes was elevated rates of *in situ* microbial activity supported by reduced compounds associated with sinking particles. *In situ* chemolithotrophic production may supplement the flux of organic material resulting from the high euphotic-zone production in the Volcano 7 region (Owen and Zeitschel, 1970).

d. Comparisons with shallow water. Downslope patterns of macrofaunal abundance and diversity on Volcano 7 bear much resemblance to those described along shallow-water organic pollution gradients (Pearson and Rosenberg, 1978). According to the Pearson and Rosenberg model (1978; their Fig. 2), low densities and low species richness are characteristic of infaunal assemblages at or very near sources of organic enrichment, while a short distance away, densities of a few tolerant, opportunistic species can be extraordinarily high, often over a very narrow spatial range. In cleaner waters, further along the enrichment gradient, infaunal density drops and diversity rises to normal values. Macrofaunal abundances on Volcano 7 exhibited a similar trend downslope. They were reduced on the oxygen-poor, organic-rich upper summit, peaked dramatically over a narrow depth range on the lower summit, and exhibited low densities on the flank and base (Fig. 6C). Diversity was lowest on the upper summit, moderately low on the lower summit, and increased relative to the other two zones on the flank and base (Fig. 10B). Dominance exhibited the reverse trend. Pearson and Rosenberg (1978) observed that species richness is sometimes highest in an 'ecotone region' between polluted and cleaner sediments. The flank, where cores tended to exhibit the highest diversity (Fig. 10B), may represent some sort of ecotone between oxygen or enrichment regimes.

Along organic pollution gradients, high-density assemblages often consist of opportunistic species (Pearson and Rosenberg, 1978). In shallow water many of these opportunistic species exhibit rapid rates of population increase, brood their larvae and have exhibit limited dispersal (Grassle and Grassle, 1974). While we have no direct evidence that the dominant species on the lower summit are opportunistic, reproductive observations are highly suggestive of opportunistic life histories. Five of the 6 dominant polychaetes on the lower summit (*Protodorvillea* sp., *Euchone incolor, Cirrophorus lyra, Caulleriella* sp., *Tharyx* sp. A) have been observed to brood larvae to late stages within brood pouches or in their tubes. Most of the polychaete individuals collected on the upper and lower summit (over 80%) belong to species shown to brood, compared to 27% on the flank and only 16% on the base (Levin, Plaia and Huggett, in preparation). Also, at the time of sampling, levels of reproductive activity were significantly higher among polychaetes on the upper and lower summit than on the flank and base (see Results section). These observations lead us to hypothesize that the polychaetes dominating the low-oxygen, food-rich summit of Volcano 7 have opportunistic life styles.

e. Paleobiological and evolutionary implications. The Volcano 7 data permit us to address several paleobiological and evolutionary problems, including biofacies models for dysaerobic (low-oxygen) communities. Rhoads and Morse (1971) proposed the existence of 3 biofacies associated with oxygen gradients: (1) an azoic zone devoid of macrofauna where O_2 is less than 0.1 ml/l, (2) a low-diversity zone inhabited by soft-bodied infauna in regions where O_2 is between 0.3 and 1.0 ml/l, and (3) a diverse community with abundant calcareous fauna where O_2 exceeds 1.0 ml/l. They suggested these communities may recapitulate the evolution of Precambrian and Cambrian invertebrates during changing oxygen conditions. Thomson *et al.* (1985) suggested modifications to the Rhoads and Morse (1971) scheme based on studies of faunal zonation in the central California OMZ. They also observed laminated sediments devoid of macroinvertebrates at O_2 levels <0.1 ml/l, but reported a low-diversity assemblage of soft-bodied infauna between 0.1 and 0.3 ml/l and abundant calcareous fauna in highly bioturbated sediments where O_2 exceeded 0.3 ml/l.

The Volcano 7 investigations revealed similar faunal gradations between the upper and lower summit in the low-oxygen interface region. Soft-bodied forms (aplacophorans, pogonophorans, and a few polychaetes) occurred at low densities (561–1,939/m^2) on the uppermost summit, with little bioturbation evident (Levin, unpublished ^{210}Pb data). A dense, low-diversity, polychaete-dominated assemblage (4,694–13,112/m^2) occurred on the lower summit, along with several abundant calcareous species (such as the serpulid polychaete *Hyalopomatus* sp.).

Although these changes occurred near oxygen concentrations of 0.1 ml/l, selecting absolute oxygen threshold values, as was done by Rhoads and Morse (1971) and Thomson *et al.* (1985), is too simplistic for the complicated and dynamic situation on Volcano 7. Here, there was overlap in the range of measured oxygen values in the two summit habitats, differences between these depths within a single CTD cast were very small (and not always in the same direction), and there was vertical displacement of water masses tidally. Flows over seamounts are complex, including such phenomena as breaking internal waves (Roden, 1987) or seamount-generated internal tides (Noble *et al.*, 1988). Physiological control of benthos at the type of dynamic oxygen interface present on Volcano 7 is likely to be a function of amplitude and temporal variation as well as absolute oxygen concentration.

There exists substantial controversy concerning the manner in which biogenic structures preserved in the fossil record vary in response to oxygen levels, and their use in reconstructing oxygenation histories of ancient marine seafloors. Ekdale and Mason (1988) suggested that trace structures should shift from a dominance of tubes under higher-oxygen conditions to (deposit) feeding traces in lower-oxygen environments. Wheatcroft (1989) proposed the opposite, based on knowledge of successional sequences associated with organic disturbance in shallow-water assemblages. The macrofauna inhabiting the lower summit of Volcano 7 (0.11 to 0.16 ml O_2/l) were dominated (55%) by three taxa (an anemone, a sabellid and a cirratulid; Appendix II) that are relatively sessile, surface-feeding forms which construct tubes or shallow burrows. These findings partially support the arguments of Wheatcroft (1989) that tube builders dominate in hypoxic conditions. However, several other taxa (20% of the total) on the Volcano 7 lower summit were shallow, subsurface, burrowing forms that are either deposit feeders or carnivorous. The sparse macrofauna inhabiting the upper summit was dominated (47%) by a presumably carnivorous aplacophoran (Lepidomeniidae). Seventy-one percent of the aplacophorans were found in the top 2 cm of sediment, but some individuals were present to a depth of 10 cm. Thus, a diversity of infaunal lifestyles, including tube builders and burrowers, are represented in the low oxygen environment on Volcano 7. It is unclear which, if any, are most likely to leave imprints in the fossil record.

5. Conclusions

(1) Faunal response (tolerance) to hypoxia on Volcano 7 varies with organism size and perhaps metabolic flexibility. Microbial and meiofaunal communities appear more tolerant than macro- and megafaunal communities. Very low oxygen concentrations appear to reduce macro- and megafaunal abundance, and influence species composition and diversity on Volcano 7, overriding other factors such as food availability and sediment grain size.

(2) Food availability, reflected by labile material such as chlorophyll *a*, appears to regulate overall abundance of bacteria and meiofauna on Volcano 7, and when oxygen is not limiting, macrofaunal abundance as well.

(3) Sediment grain size and percent organic carbon are correlated with bacterial abundance but do not appear to influence macrofaunal community structure on Volcano 7.

(4) Macrofaunal abundance and diversity patterns along an oxygen/enrichment gradient at the lower boundary of the OMZ on Volcano 7 resemble those typically observed for macrofauna along gradients of organic pollution in shallow waters.

(5) Dysaerobic (low oxygen) macrofaunal assemblages have a species composition distinct from fully aerobic assemblages and include predominantly surface- (suspension and deposit) feeding forms that construct permanent tubes or burrows in the top few centimeters of sediments.

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APPENDIX I

Samples involved in physical, chemical and biological analysis of sediments. See Figure 1 for location of samples.

Dive	Depth	Grain Size	$CaCO_3$	POC PON C:N	Chlorophyll *a* Phaeopigments	Bacteria	Meio-fauna	Macro-fauna	Megafauna (No. Photos)
2141	US	1TC	1TC	1TC	1TC	1TC	2BC	2BC	144
2149	US	2TC	1TC	1TC	1TC	2TC	2BC	2BC	66
2150	US	1TC	1TC	1TC	—	1TC	2BC	2BC	47
1392	LS	1TC	1TC	1TC	1TC	—	—	2BC	—
2139	LS	1TC	1TC	1TC	1TC	1TC	2BC	2BC	44
2140	LS	1TC	1TC	1TC	1TC	1TC	—	—	106
2141	LS	1TC	1TC	1TC	—	—	—	—	70
2142	LS	—	—	—	—	—	—	—	61
2149	LS	—	—	—	—	—	—	—	60
2150	LS	—	—	—	—	—	—	—	5
A224*	LS	—	—	—	—	—	—	—	383
1393	F	2TC	1TC	1TC	1TC	—	—	2BC	—
2143	F	1TC	1TC	1TC	1TC	1TC	2BC	2BC	48
2144	F	1TC	1TC	1TC	1TC	1TC	1BC	1BC	51
2145	F	1TC	1TC	1TC	1TC	2TC	2BC	2BC	20
A224*	F	—	—	—	—	—	—	—	725
2146	B	1TC	—	—	—	—	2BC	2BC	35
2147	B	2TC	1TC	1TC	1TC	2TC	2BC	2BC	55
2148	B	1TC	1TC	1TC	1TC	2TC	2BC	2BC	55
1394	B	1TC	—	1TC	1TC	—	—	2BC	—
1395	B	1TC	1TC	1TC	—	—	—	2BC	—
A226*	B	—	—	—	—	—	—	—	388

US = Upper Summit, LS = Lower Summit, F = Flank, B = Base.
TC = *Alvin* Tubecore, BC = Boxcore
**Angus* Tows from 1984

APPENDIX II

Macrofauna (>300 μm) composition of Volcano 7 sediments. Mean no. per 196 cm^2 core ± 1 S.D.

	Upper Summit (745–767 m) $n = 6$	Lower Summit (788–857 m) $n = 4$	Flank (1316–1790 m) $n = 7$	Base (2850–3353 m) $n = 10$	Feeding Guild
POLYCHAETA					
ACROCIRRIDAE					
sp. A		0.25 ± 0.50	1.00 ± 1.53	0.50 ± 1.27	SDF
sp. B			0.40 ± 0.38	0.10 ± 0.32	SDF
AMPHARETIDAE					
Ampharete sp.		8.50 ± 3.87	0.14 ± 0.38		SDF
sp. B		0.75 ± 0.96	1.29 ± 1.98	0.10 ± 0.32	SDF
sp. C		0.50 ± 1.00			SDF
sp. D		0.25 ± 0.50			SDF
sp. E			0.14 ± 0.38		SDF
CAPITELLIDAE					
sp. A			0.14 ± 0.38		SSDF
Notomastus tenuis			0.29 ± 0.76		SSDF
CHRYSOPETALIDAE					
Dysponetus sp.			0.29 ± 0.76	0.10 ± 0.32	C/S
Dysponetus sp. A				0.20 ± 0.42	C/S
Dysponetus sp. B		0.50 ± 0.58			C/S
sp. A			0.14 ± 0.38		C/S
CIRRATULIDAE					
Caulleriella sp. 1		13.00 ± 5.94			SDF
Caulleriella sp. 2	0.17 ± 0.41		0.43 ± 0.79		SDF
Chaetozone sp.		0.25 ± 0.50		0.90 ± 1.45	SDF
Tharyx sp. A	1.00 ± 1.26	28.65 ± 8.62	0.57 ± 1.13	0.70 ± 1.06	SDF
Tharyx sp. B			1.14 ± 1.46	0.20 ± 0.63	SDF
Unidentified spp.*		0.75 ± 0.96	0.43 ± 0.53	0.30 ± 0.48	SDF

DORVILLEIDAE					
Dorvillea sp. A				0.40 ± 0.70	C/S
Protodorvillea sp. A	2.83 ± 1.60	14.25 ± 15.37			C/S
Protodorvillea sp. B			1.00 ± 1.41	0.30 ± 0.67	C/S
EUNICIDA					
sp. A			0.14 ± 0.38		*
EUNICIDAE					
sp. A		0.25 ± 0.50			C/S
EUPHROSINIDAE					
Euphrosine sp.			0.51 ± 1.50		C/S
FAUVELIOPSIDAE					
Fauveliopsis sp.				0.10 ± 0.32	SSDF
FLABELLIGERIDAE					
Diplocirrus sp.				0.10 ± 0.32	SDF
Flabelliderma sp.	0.17 ± 0.41	0.25 ± 0.50		0.10 ± 0.32	SDF
Flabelligera sp.		1.00 ± 2.00	0.14 ± 0.38		SDF
sp. A			0.14 ± 0.38		*
GLYCERIDAE					
Glycera sp.			0.57 ± 0.78		SSDF/C
sp. B				0.40 ± 0.97	SSDF/C
HESIONIDAE					
Bonuania sp.	1.33 ± 1.21	2.50 ± 2.52	0.14 ± 0.38		C/S
Syllidia sp.			1.14 ± 1.07		C/S
sp. A				0.20 ± 0.42	C/S
LUMBRINERIDAE					
Lumbrineris sp. A				0.30 ± 0.48	C/S
Lumbrineris sp. C			0.29 ± 0.76		C/S
Lumbrineris laguna		0.25 ± 0.50	0.57 ± 0.79		C/S
MALDANIDAE					
sp. A			1.00 ± 1.15		SSDF

NEPHTYIDAE					
Aglaophamus sp.				0.80 ± 0.92	C/S
sp. C				0.10 ± 0.32	C/S
NEREIDAE					
sp. A				0.60 ± 0.84	C/S
OPHELIIDAE					
nr. *Ammotrypane* sp.			0.29 ± 0.49	0.50 ± 1.08	SSDF
Ophelia sp.			0.14 ± 0.38		SSDF
ORBINIDAE					
sp. A			0.29 ± 0.76		SSDF
Leitoscoloplos sp.				0.20 ± 0.42	SSDF
OWENIIDAE					
Myrowenia sp.			0.14 ± 0.38		SDF
QUESTIDAE					
sp. A			0.14 ± 0.38	0.10 ± 0.32	SDF
PARAONIDAE					
Aricidea (Acmira) cerrutii			0.14 ± 0.38	0.10 ± 0.32	SSDF
Aricidea (Acmira) lopezi				0.60 ± 1.07	SSDF
Aricidea (Acmira) sp. C			0.14 ± 0.38	0.10 ± 0.32	SSDF
Aricidea (Aedicira) sp. A				0.20 ± 0.42	SSDF
Aricidea (Allia) quadrilobata			0.71 ± 1.11	0.40 ± 0.70	SSDF
Aricidea (Allia) sp. B			0.29 ± 0.49		SSDF
Aricidea (Allia) sp. E		0.25 ± 0.50	0.14 ± 0.38	0.20 ± 0.42	SSDF
Aricidea (Aricidea) sp. A			0.14 ± 0.38	0.10 ± 0.32	SSDF
Aricidea (Aricidea) minuta			0.14 ± 0.38		SSDF
Cirrophorus lyra	6.50 ± 9.87	17.25 ± 17.21			SDF

Cirrophorus sp. 2		1.43 ± 1.99		SDF
Levinsenia cf *gracilis*			0.50 ± 0.71	SDF-
Levinsenia uncinata			0.10 ± 0.32	SSDF
sp. G		0.71 ± 1.11	0.30 ± 0.67	*
Unidentified spp.*	0.50 ± 0.58	0.29 ± 0.49	0.50 ± 0.71	*
PHYLLODOCIDAE				
nr. *Eteone* sp.		0.29 ± 0.76	0.10 ± 0.32	C/S
PILARGIDAE				
nr. *Synelmis* sp.		0.29 ± 0.49	0.10 ± 0.32	C/S
SABELLIDAE				
Euchone incolor	26.50 ± 0.95	0.57 ± 0.79	0.90 ± 0.91	FF
Fabrisabella similis		2.00 ± 2.31	0.70 ± 1.06	SDF/FF
sp. B		0.43 ± 0.79	0.10 ± 0.32	*
Unidentified spp.	0.25 ± 0.50	0.14 ± 0.38		*
SCALIBREGMATIDAE				
sp. C		0.14 ± 0.38		SSDF
SERPULIDAE				
Serpula sp.			0.30 ± 0.67	FF
nr. *Protula* sp.		0.29 ± 0.76	0.20 ± 0.63	FF
SIGALIONIDAE				
Leanira sp.			0.10 ± 0.32	C/S
nr. *Stenolepsis* sp.			0.10 ± 0.32	C/S
SPHAERODORIDAE				
Sphaerodorum sp.			0.10 ± 0.32	SSDF
Sphaerephesis sp.		0.14 ± 0.38		SSDF
SPIONIDAE				
Prionospio (Minuspio) sp.		1.14 ± 1.46		SDF/FF
Laonice sp.		0.14 ± 0.38		SDF/FF
sp. C		0.14 ± 0.38	0.10 ± 0.32	SDF/FF
sp. D		0.14 ± 0.38		*

SYLLIDAE					
Atelesyllis sp.			0.57 ± 1.13	0.90 ± 0.99	C/S
sp. B			0.43 ± 1.13	0.20 ± 0.42	*
sp. C			0.14 ± 0.38	0.30 ± 0.67	*
sp. E				0.10 ± 0.32	*
TEREBELLIDAE					
Unidentified spp.*			2.00 ± 2.00	0.20 ± 0.42	SDF
nr. HESIONIDAE			0.14 ± 0.38		
nr. NEREIDAE				0.10 ± 0.32	*
nr. SPHAERODORIDAE				0.10 ± 0.32	*
Unidentified spp.*				0.40 ± 0.84	*
TOTAL POLYCHAETES	**12.00 ± 12.77**	**117.25 ± 30.09**	**26.29 ± 11.91**	**15.50 ± 7.68**	
TOTAL POLYCHAETE SPP.	**6**	**19**	**53**	**49**	
OLIGOCHAETE				0.20 ± 0.42	
NEMERTEA					
sp. A		0.75 ± 0.96	1.43 ± 1.40	1.20 ± 1.62	
sp. B		1.25 ± 1.50	0.57 ± 1.13	0.20 ± 0.42	
SIPUNCULA					
Golfingia sp.			1.14 ± 0.69	0.10 ± 0.32	
Unidentified spp.*				0.40 ± 0.97	
PRIAPULIDA			0.14 ± 0.38	0.30 ± 0.48	
POGONOPHORA	3.17 ± 2.79				
Unidentified Vermes sp. A			0.14 ± 0.38	1.00 ± 1.33	
Unidentified Vermes sp. B	0.33 ± 0.82		0.14 ± 0.38		

MOLLUSCA				
APLACOPHORA				
Chaetodermomorpha				
Lepidomeniidae	17.17 ± 9.28	0.50 ± 0.58	0.71 ± 0.76	
Limfossor sp.				0.10 ± 0.32
Neomeniomorpha		0.50 ± 0.58	0.14 ± 0.38	0.10 ± 0.32
Unidentified spp.	0.17 ± 0.41		0.29 ± 0.49*	
BIVALVIA				
sp. A	1.33 ± 1.63	7.25 ± 3.20	1.43 ± 1.27	0.30 ± 0.48
sp. B				0.20 ± 0.63
sp. C				0.10 ± 0.32
sp. D				0.10 ± 0.32
Cuspidaridae		0.25 ± 0.50	0.29 ± 0.49	
GASTROPODA				
sp. A			1.86 ± 2.12	0.10 ± 0.32
sp. B			0.29 ± 0.49	
SCAPHOPODA	0.17 ± 0.41	0.25 ± 0.50	0.14 ± 0.38	
TOTAL MOLLUSCA	**18.83 ± 9.85**	**8.75 ± 2.75**	**5.14 ± 2.48**	**1.00 ± 1.05**
TOTAL MOLLUSCA SPP.	**4**	**5**	**7**	**7**
CRUSTACEA				
AMPHIPODA				
LYSIANASSIDAE				
Pachynus group			0.14 ± 0.38	
PARDALISCIDAE				
nr. *Halice*			1.29 ± 1.50	0.10 ± 0.32
PHOXOCEPHALIDAE				
Heterophoxus sp.			0.14 ± 0.38	
Unidentified spp.*				0.20 ± 0.42

ISOPODA		
DENDROTIIDAE		
sp. A		1.50 ± 2.42
DESMOSOMATIDAE		
sp. A		0.60 ± 1.26
EURYCOPIDAE		
Belonectes sp.		0.90 ± 1.66
Syneurycope sp.		0.30 ± 0.48
ILYARCHNIDAE		
Ilyarchna sp.		0.20 ± 0.63
JANIRIDAE		
cf *Astronicus*	0.14 ± 0.38	0.30 ± 0.67
NANNONISCIDAE		
Hebefustis sp.	0.86 ± 1.46	
PARAMINNIDAE		
Notoxenoides sp.	0.14 ± 0.38	
TANAIDACEA		
LEPTOGNATHIDAE		
Leptognathia sp. BB		0.50 ± 1.58
Leptognathia sp. NNNN	0.14 ± 0.38	0.10 ± 0.32
Leptognathia sp. MMMM		0.10 ± 0.32
Leptognathia sp. OO		0.20 ± 0.63
Leptognathia voringii	0.14 ± 0.38	0.40 ± 0.70
Leptognathidae sp.		0.30 ± 0.95

Filitanais sp. GG				2.70 ± 3.83
PSEUDOTANAIDAE				
Pseudotanais sp.				1.20 ± 3.46
CUMACEA				0.10 ± 0.33
UNIDENTIFIED CRUSTACEA		0.25 ± 0.50		
TOTAL CRUSTACEANS	**0.00**	**0.25 ± 0.50**	**3.00 ± 3.32**	**9.70 ± 6.52**
TOTAL SPECIES	**0**	**1**	**8**	**16**
ECHINODERMATA				
HOLOTHUROIDEA				
sp. A			0.29 ± 0.76	
sp. B				0.30 ± 0.48
OPHIUROIDEA				
sp. A	0.33 ± 0.52	0.75 ± 0.96	1.43 ± 1.51	
sp. B			1.14 ± 1.46	
ECHINOIDEA				
sp. A				0.30 ± 0.95
PORIFERA			0.71 ± 0.76	
HYDROID (colony)		0.25 ± 0.50	0.14 ± 0.38	
ANEMONE		35.25 ± 46.89	0.57 ± 1.13	0.10 ± 0.32
ACARINA				0.10 ± 0.32
PYCNOGONIDA		0.75 ± 1.50		
BRACHIOPODA				0.10 ± 0.32
BRYOZOA (colony)				0.20 ± 0.42
TUNICATE				0.10 ± 0.32
CHAETOGNATHA	1.67 ± 1.86	0.50 ± 1.00	0.14 ± 0.38	0.80 ± 1.40
TOTAL OTHER	**24.33 ± 9.35**	**48.50 ± 47.02**	**16.14 ± 9.04**	**16.10 ± 8.79**
TOTAL MACROFAUNA	**36.33 ± 17.20**	**165.75 ± 73.87**	**42.43 ± 18.74**	**31.60 ± 15.70**
MINIMUM TOTAL SPP.	**14**	**32**	**81**	**86**

*Not included in species totals.

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