Involvement of the oxygen minimum in benthic zonation on a deep seamount

Karen Wishner, Lisa Levin*, Marcia Gowing† & Lauren Mullineaux‡

Graduate School of Oceanography, University of Rhode Island, Narragansett, Rhode Island 02882, USA
* Department of Marine, Earth, and Atmospheric Sciences, North Carolina State University, Raleigh, North Carolina 27695-8208, USA
† Institute of Marine Sciences, University of California, Santa Cruz, California 95064, USA
‡ Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543, USA

LOW oxygen concentration in the seawater column reduces the abundance of midwater consumer populations[1,2], which can enhance the supply of undegraded organic matter reaching the benthos. Low oxygen concentration in the water at the bottom can exclude most tolerant species from benthic habitats[3-5]. The interception of the seafloor with pronounced oxygen-minimum zones can produce steep gradients in benthic assemblages. We now present evidence for this interaction on Volcano 7, an oceanic seamount penetrating the oxygen-minimum zone in the eastern tropical Pacific. Submersible observations revealed only a few benthic species at the summit (730–750 m), where oxygen levels were lowest. Just tens of metres below, megafaunal and macrofaunal abundances were extremely high. Sediment organic carbon, a benthic food indicator, was unusually high. We hypothesize that a dynamic low-oxygen interface physiologically restricts benthos on the upper summit, that the enriched sediment is a result of reduced consumption and degradation of sinking material in the oxygen-minimum zone, and that this high benthic food level supports the unusually high benthic abundance. Sharp benthic zonation associated with oxygen concentrations may also be preserved in the palaeoceanographic record[4,6].

Volcano 7, an inactive seamount[7] at 13° 23′ N, 102° 27′ W, of 20-km diameter, rises from a depth of 3,400 m to 730 m. Its benthic and pelagic ecology were studied with submersible and shipboard sampling (including conductivity temperature depth (CTD) hydrocasts, water samples, box cores, photography, plankton tows, current meters and sediment traps) on a cruise in November 1988. Benthic data from June 1984 are also discussed.

The eastern tropical Pacific is characterized by a shallow mixed layer and a pronounced oxygen minimum[8]. At the Volcano 7 site, the mixed layer was 22 m deep, and the base of the euphotic zone was at 85 m. Sharp peaks of fluorescence, particles, chlorophyll *a*, phytoplankton, protozoans and zooplankton occurred just below the mixed layer (Fig. 1). The core of the oxygen minimum zone (oxygen <0.5 ml per litre of seawater) occurred from median depths of 72–1302 m, and the lowest oxygen (≤0.1 ml per litre) from median depths of 288–1,077 m (Fig. 1*a*). Thus the base of the euphotic zone was within the oxygen-minimum zone, and particles sinking out of the euphotic zone immediately entered a broad region of low oxygen and reduced plankton abundance.

There is evidence that undegraded surface-derived material reached the seamount summit. Bottom-moored particle interceptor traps[9,10] collected intact microplanktonic organisms common in surface waters. Excess Pb-210 activity profiles[11] indicated high sedimentation rates on the summit of 0.3–0.7 mm yr^{-1}. Sediment organic carbon (up to 3.9%), organic nitrogen (up to 0.55%), chlorophyll *a* (up to 25 $\mu g\ g^{-1}$) and sediment bacterial abundances were remarkably high on the summit, especially at depths <770 m (Fig. 2). Here, C/N ratios were near 7.0 (Fig. 2*c*), indicating the presence of fresh organic matter[12]. Green flocculent material was present on the bottom in both November 1988 and June 1984. The supply of undegraded organic material to the benthos may be more continuous in this region of reduced seasonality[13] than in higher latitudes, where benthic fluxes are strongly seasonal[14,15].

Strong megafaunal zonation was observed on the summit of the seamount (Figs 3 and 4). The uppermost summit (<750 m) was visibly depauperate (Fig. 3*a* and *b*). Gradual increases in megafauna occurred in a transition zone from 750–770 m.

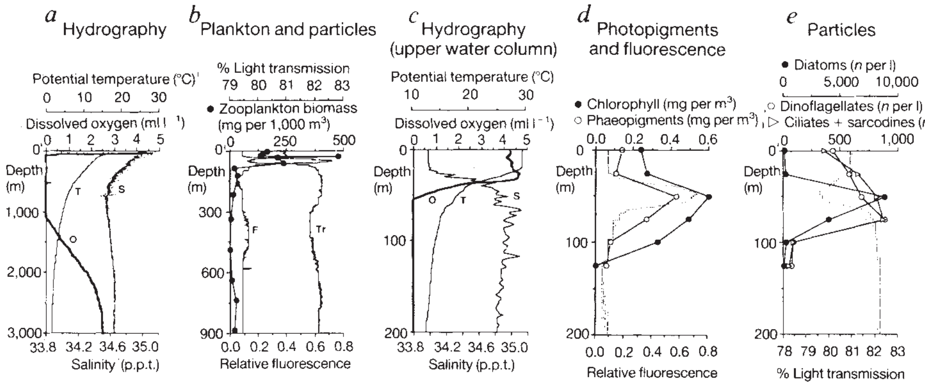

FIG. 1 Vertical profiles through the water column of physical, biological and chemical parameters. The sharp shallow thermocline is also an abrupt transition from oxygenated mixed-layer water to the very low-oxygen water in the oxygen-minimum zone. Concentrations of organisms (day and night), photopigments and particles peak sharply within the thermocline, then drop abruptly to low levels in the oxygen-minimum zone. 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[26] on individual water samples from hydrocasts, and the oxygen values from the CTD electrode were transformed on the basis of a linear equation relating the two sets of measurements. Thirty-one CTD casts were made at locations on the seamount and along north–south and east–west transects extending up to 40 km from the summit. Data from the downcast of a representative CTD profile above the seamount are shown in *a* (whole water column) and *c* (upper 200 m detail). Zooplankton were obtained in 15 vertically stratified tows (nine samples per tow) at various locations on and near the seamount by a 1 m^2 MOCNESS (ref. 27) multiple opening and closing plankton net system using 335-μm mesh nets. Wet-weight zooplankton biomasses from a night-time tow series above the seamount are plotted in *b*. Relative fluorescence was measured by a Sea Tech *in situ* fluorometer and % light transmission by a Sea Tech 25-cm beam transmissometer, both attached to the MOCNESS. Representative profiles are shown in *b* and *e*. Fluorescence and light transmission data shown in *b* were smoothed with a five-point running mean. Fluorescence data in *d* were smoothed with a three-point running mean. Chlorophyll *a* and phaeophytin values (*d*), from water overlying the seamount, are means of two or three water samples per depth with two 500-ml aliquots per sample. Measurements were made fluorometrically[28] on water collected with Niskin bottles and filtered onto GFF filters. Abundances of diatoms, dinoflagellates and ciliate plus sarcodine protozoa (*e*) are means of three counts from water overlying the seamount (*n* per litre). Aliquots of 100 ml were drawn from Niskin bottles, preserved with Lugol's iodine, settled in settling chambers, and the entire sample was counted under an inverted microscope (magnification, ×170).

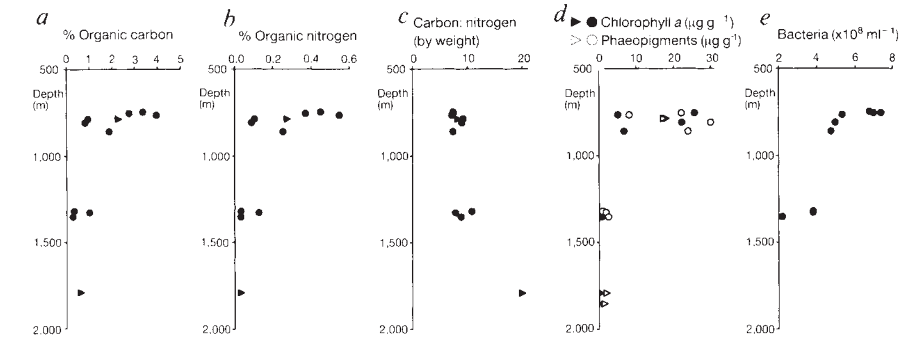

FIG. 2 Sediment organic matter properties. 1984 data, ▲; 1988 data, ●. Analyses of organic carbon (*a*), nitrogen (*b*), C/N (*c*), and chlorophyll *a* (▲, ●) and phaeopigments (△, ○) (*d*) were made on sediments collected by the submersible in tube cores and frozen at −70 °C. Organic C and N were analysed on the 0–2 cm vertical fraction. Sediments were homogenized, dried and ground, inorganic carbon was leached with 10% phosphoric acid for 24 h, then sediments were rinsed with organic-free distilled water, centrifuged, and the supernatant was decanted. The leaching process was repeated three times and remaining sediments were freeze-dried, weighed, ground and analysed on a Carlo Erba elemental analyser. Sediment chlorophyll *a* and phaeopigments were determined for 3 g sediment from the upper 1 cm using the spectrophotometric method[28] modified for sediments. Immediately on retrieval of tube cores, sediment bacteria (*e*) (1 ml from the top 1 cm) were sampled and preserved in 9 ml of 2.5% glutaraldehyde. Counts were made in the laboratory within two months of collection, using acridine-orange staining and epifluorescence microscopy[29]. There were significant differences (by analysis of variance) between upper (<770 m) and lower (770–900 m) summit locations for organic C ($P=0.015$) and N ($P=0.012$). Differences between summit (combined) and flank values were observed for organic C ($P=0.027$), organic N ($P=0.023$), chlorophyll *a* ($P=0.009$), phaeopigments ($P=0.001$) and bacteria ($P=0.004$).

Extraordinarily high densities (up to 19 individuals per m^2 in patches) occurred from 780–1,000 m, with maxima from 800–810 m (Figs 3*c*, *d* and 4*a*–*f*). Below 1,000 m, average megafaunal abundances (excluding xenophyophores) never exceeded 0.5 per m^2. This zonation did not correspond to the distribution of hard and soft substrates, and no hydrothermal activity was observed.

Abundance patterns of infauna, obtained in Ekman-style box cores, differed with size. Macrofauna (>300 μm) were rare above 750 m, with only low-oxygen-tolerant forms[16,17] present. Macrofauna increased greatly from the uppermost zone to 800–1,000 m (8,444 per m^2), then declined downslope (Fig. 4*g*). Meiofauna (smaller infauna), which are more tolerant than macrofauna to hypoxia[18], were most abundant at depths <750 m (202, 100 per m^2, $n=2$) (Fig. 4*h*). The nematode to harpacticoid copepod ratio, an indicator of oxygen stress[19], was 546:1 on the uppermost summit and declined to 1.3:1 on the flank (Fig. 4*i*).

Oxygen in near-bottom water samples obtained by submersible was 0.08–0.09 ml per litre ($n=2$,733–746 m) in the uppermost summit region of low megafaunal and macrofaunal abundance and 0.11–0.16 ml per litre ($n=3$,806–815 m) in the region of highest abundance. In five of six seamount CTD casts, oxygen was lower at 730 m than at 800 m, but there was considerable overlap in the concentration range measured at these two depths. Diurnal and semidiurnal temperature fluctuations (0.5 °C) occurred at the summit, indicating that internal tides were displacing water masses. This suggests that benthic organisms on the summit were exposed to periodically varying oxygen rather than to constant oxygen concentrations. Physiological exclusion of benthos at dynamic oxygen interfaces may therefore be a function of amplitude and temporal variation as well as absolute oxygen concentrations.

Very low plankton abundances are associated with oxygen minimum zones in the water column in parts of the Arabian Sea and the eastern Pacific, but only where oxygen is less than about 0.15 ml per litre throughout a broad depth interval[1,2], similar to the Volcano 7 region. At locations with more oxygen, plankton biomass may not be reduced, although distributions may be altered[1,20–22]. For midwater crustaceans, an oxygen concentration of 0.13 ml per litre is a critical lower oxygen limit for

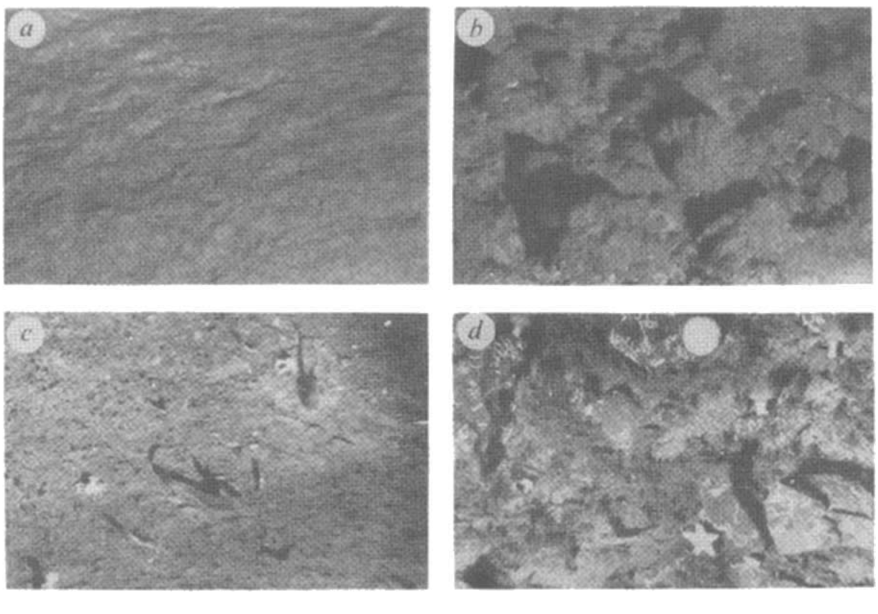

FIG. 3 Representative photographs of the upper summit (*a*, *b*; 744 and 734 m respectively) and lower summit (*c*, *d*; 770 and 780 m respectively). *a* and *c* show foraminiferal sand substrate, whereas *b* and *d* show rocky and mixed substrate. The only megafauna on the upper summit (*a*, *b*) were occasional rattail fish (*Nezumia liolepis*, shown in *c* and *d* but not in upper summit photographs) and solitary sessile coelenterates under rocks (White dots in *b*). Rock surfaces appear fuzzy (*b*, *d*) because of dense mats of an unidentified tube-building protozoan. Dark green detrital material was visible on rocks and sediments. Upper summit (*a*) meiofauna included large numbers of nematodes. The most abundant macrofauna were an aplacophoran (family Lepidomeniidae), a paraonid polychaete (*Cirrophorus lyra*), a dorvilleid polychaete (*Protodorvillea* sp.) and a few pogonophorans. A variety of abundant megafauna occurred on both rocks and sediments on the lower summit (*b*, *d*). Rattail fish (*N. liolepis*), galatheid crabs (*Munidopsis c.f. hystrix*), shrimp, starfish, sponges, anemones, ophiuroids and serpulid worm tubes (*Hyalopomatus marenzelleri*) are some of the organisms in *c* and *d*. Here, dark green or green-grey flocculent material occurred in depressions. Infaunal densities were high for sand substrates (>8,000 per m^2), and dominant infauna included cirratulid, sabellid and dorvilleid polychaetes and burrowing anemones. These photographs were taken with a hand-held 35-mm camera from inside the *Alvin* submersible and show an area of 2–3 m^2. For scale, the galatheid crabs are about 5 cm from claw tip to tail.

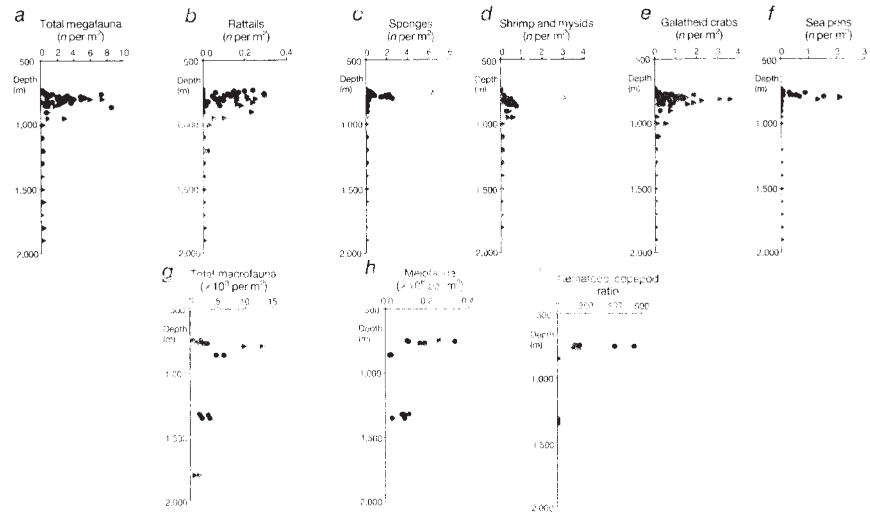

FIG. 4 Benthic faunal densities on the summit and flank as a function of water depth. 1984 data, ▲; 1988 data, ●. Megafaunal abundances were quantified from 1988 *Alvin* photographs (external hull-mounted camera) using a perspective grid to calculate surface area, and from 1984 *Angus* camera sled photographs, in which area was calculated as 1.25 sled altitude ×1.8 sled altitude. Mean faunal densities are shown for 10-m depth intervals 730–850 m, for 50-m intervals 850–1,000 m, and for 100-m intervals 1,000–2,000 m. Data from photographs taken on different parts of the seamount (at comparable depths) are plotted separately. Maximum densities of major taxa (1984 photographs) were 4.3 per m^2 for sponges, 9.7 per m^2 for galatheid crabs, 7.3 per m^2 for combined shrimp and mysids, 1.8 per m^2 for rattail fishes and 4.9 per m^2 for sea pens. For analysis of variance statistics, the upper summit includes data from 730–770 m and the lower summit, from 770–1,000 m. *a*, Total megafauna, excluding xenophyophores and the solitary coelenterates attached to rock bases on the upper summit. These groups were excluded because they were not reliably visible in *Angus* photographs. There were significant differences between the upper and lower summit ($P=0.036$) and the summit and flank ($P<0.001$). *b*, Rattail fishes (*N. liolepis*). Fish were ~15–20 cm long. There were significant differences between the upper and lower summit ($P=0.033$) and between the summit and flank ($P<0.001$). *c*, Total sponges. At least three unidentified species were present. There were significant differences between the summit and flank ($P=0.020$). *d*, Combined shrimp (*Heterocarpus nesisi* and *Benthescymus altus*) and mysids (*Boreomysis* sp.). Nearly significant differences were observed between summit and flank sites ($P=0.066$). *e*, Galatheid crabs (*M. c.f. hystrix*). Crabs are ~5-cm long. There were significant differences between upper and lower summit sites ($P=0.003$) and between summit and flank sites ($P<0.001$). *f*, Unidentified sea pens. These were present only on soft substrates and were ~15-cm long. *g*, Total macrofauna retained on a 300-μm screen. Samples were taken in Ekman-style box cores (196 cm^2 surface area) to a depth of 15 cm. Samples were preserved on board ship in 10% buffered formalin and later transferred to alcohol and sorted in the laboratory. Each data point represents macrofauna from one box core converted to *n* per m^2. There were significant differences between upper and lower summit sites ($P=0.003$) and between summit and flank sites ($P=0.051$). *h*, Total meiofauna (excluding foraminifera) retained on a 63-μm screen. Samples were taken from one subcore (49 cm^2 surface area) within each box core, processed as described above. Only the upper 5 cm of sediment were sorted for meiofauna. There were significant differences between the upper and lower summit ($P=0.044$). *i*, Nematode to harpacticoid copepod abundance ratios in the meiofauna cores. There were significant differences between summit and flank sites ($P=0.019$).

aerobic metabolism, although some vertical migrators can transit narrow low oxygen zones, or live anaerobically or at very low metabolic levels (in diapause, for example) for periods of time[23]. A pronounced oxygen-minimum zone that is vertically broad is therefore an effective barrier for most plankton. In this situation, the use of particulate material in midwater would be reduced, presumably enhancing benthic particulate fluxes.

Other interactions between the seamount and flow field could also mediate effects of the oxygen minimum. The high regional productivity of the eastern tropical Pacific[13] could be supplemented near Volcano 7 by topographically induced upwelling[24], which could contribute to the particle flux to the benthos. But, no definitive evidence of upwelling into the euphotic zone (which already extended below the mixed layer) was observed. Current acceleration over topographic features is an alternative process that may enhance local abundances of suspension-feeding megafauna on seamounts[25]. Although high abundances of some species occurred on ridges, the general megafaunal abundance peak on the summit of Volcano 7 did not correspond to exposed topography and included many non-suspension-feeding taxa.

We hypothesize that the striking benthic zonation on Volcano 7 is due to effects of the oxygen-minimum operating both in the water column (by enhancement of undegraded particulate food supply) and on the benthos (by exclusion of hypoxia-sensitive taxa). Oxygen minima also intersect the sea floor on continental slopes, as in the Arabian Sea[5], and the distinctive benthic faunal gradients produced by these interactions could be preserved in the palaeoceanographic record[4,6]. □

Received 13 February; accepted 20 April 1990.

1. Longhurst, A. R. *Deep-Sea Res.* **14,** 51–63 (1967).
2. Vinogradov, M. E. & Voronina, N. M. *Okeanologiya* **1,** 670–678 (1961). English translation in *Deep-Sea Res.* **9,** 523–530 (1962).
3. Sanders, H. L. in *Diversity and Stability in Ecological Systems,* 71–81 (Brookhaven National Laboratory, Upton, New York, 1969).
4. Rhoads, D. C. & Morse, J. W. *Lethaia* **4,** 413–428 (1971).
5. Rice, A. L. (ed.). *Deep-Sea Challenge: The John Murray/"Mabahiss" Expedition to the Indian Ocean, 1933–34* (Unesco, Paris, 1986).
6. Mullins, H. T., Thompson, J. B., McDougall, K. & Vercoutere, T. L. *Geology* **13,** 491–494 (1985).
7. Batiza, R. *Geology* **8,** 477–482 (1980).
8. Wyrtki, K. *Oceanogr. mar. Biol. a. Rev.* **4,** 33–68 (1966).
9. Knauer, G. A., Martin, J. H. & Bruland, K. W. *Deep-Sea Res.* **26,** 97–108 (1979).
10. Gowing, M. M. & Silver, M. W. *Mar. Biol.* **73,** 7–16 (1983).
11. DeMaster, D. J., McKee, B. A., Nittrouer, C. A., Brewster, D. C. & Biscaye, P. E. *Mar. Geol.* **66,** 133–148 (1985).
12. Banse, K. *Limnol. Oceanogr.* **19,** 695–699 (1974).
13. Owen, R. W. & Zeitschel, B. *Mar. Biol.* **7,** 32–36 (1970).
14. Lampitt, R. S. *Deep-Sea Res.* **32,** 885–897 (1985).
15. Deuser, W. G. *Deep-Sea Res.* **33,** 225–246 (1986).
16. Southward, A. J. & Southward, E. C. *ISI Atlas of Science: Animal and Plant Sciences* **1,** 203–207 (1988).
17. Levin, L. A. & Smith, C. R. *Deep-Sea Res.* **31,** 1277–1285 (1984).
18. Josefson, A. B. & Widbom, B. *Mar. Biol.* **100,** 31–40 (1988).
19. Raffaelli, D. *Mar. envir. Res.* **23,** 135–152 (1987).
20. Sewell, R. B. S. & Fage, L. *Nature* **162,** 949–951 (1948).
21. Brinton, E. *Prog. Oceanogr.* **8,** [illegible]–139 (1979).
22. Sameoto, D. D., Guglielmo, L. & Lewis, M. K. *Mar. Biol.* **96,** 235–245 (1987).
23. Childress, J. J. *Comp. Biochem. Physiol.* **50A,** 787–799 (1975).
24. Boehlert, G. W. & Genin, A. in *Seamounts, Islands and Atolls* (eds Keating, B. H., Fryer, P., Batiza, R. & Boehlert, G. W.) 319–334 (American Geophysical Union, Washington, DC, 1987).
25. Genin, A., Dayton, P. K., Lonsdale, P. F. & Spiess, F. N. *Nature* **322,** 59–61 (1986).
26. Carritt, D. E. & Carpenter, J. H. *J. mar. Res.* **24,** 286–318 (1966).
27. Wiebe, P. H., Burt, K. H., Boyd, S. H. & Morton, A. W. *J. mar. Res.* **34,** 313–326 (1976).
28. Parsons, T. R., Maita, Y. & Lalli, C. M. *A Manual of Chemical and Biological Methods for Seawater Analysis* (Pergamon, Oxford, 1984).
29. Hobbie, J. E., Daley, R. J. & Jasper, S. *Appl. envir. Microbiol.* **33,** 1225–1228 (1977).

ACKNOWLEDGEMENTS. We thank the *Alvin* pilots, *R/V Atlantis II* crew and master, and all the scientists participating in the cruise. Special thanks to C. Ashjian, R. Batiza, L. Beatty, S. Coale, N. Craig, C. Gelfman, R. Hinegardner, D. Huggett, L. Kann, C. Mann, D. Nelson, J. Schoenherr, C. Thomas, D. Vanko and J. Wormuth. This work was supported by the NSF and the Office of Naval Research.