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Feeding ecology of benthopelagic zooplankton on an eastern tropical Pacific seamount

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Abstract. The gut contents of dominant deep-sea benthic boundary layer zooplankton (primarily copepods and mysids) and the vacuole contents of phaeodarians collected and preserved in situ at four depths (from 724 to 3112 m) on an eastern tropical Pacific seamount (Volcano 7; 13°23'N, 102°27'W) between 23 November and 4 December 1988 were analyzed using transmission electron microscopy (TEM). Suspended, and sinking plus resuspended particles, were quantitatively sampled to characterize potential food sources. The broad oxygen minimum characteristic of this region intersects the summit of the seamount and affects the feeding ecology of these organisms. Several copepods and mysids and an amphipod contained guts packed with what appeared to be gram-positive bacteria, an unusual finding. We hypothesize that the source of these bacteria-like bodies was a mat or aggregate that originated in the oxygen minimum or at its upper or lower interface. The presence of the bacteria-like bodies in 43 to 100% of the particle-feeding zooplankton that were sectioned and that had gut contents, suggests that the bacteria-like bodies are an important food source. The diverse gut and vacuole contents of other detritivores were similar among depths. Particles and microorganisms from the depths were also similar. This finding can be explained by the rapid sinking of particles and aggregates from surface waters and their relatively intact transit through the broad oxygen minimum with its reduced populations of zooplankton. The presence of algal cells in guts and vacuoles of benthic boundary-layer zooplankton suggests that these zooplankton select particles of recent surface origin for consumption. The presence of the guts filled with bacteria-like bodies shows that some deep-sea copepods and mysids that are normally generalist feeders can specialize opportunistically. The similarity of gut contents of crustaceans and vacuole contents of phaeodarians suggests that these two very different groups of particle feeders utilize similar food sources in the deep sea.

Introduction

Zooplankton of the benthic boundary layer of the deep sea live in an environment of elevated particle concentrations and zooplankton biomass (e.g. Wishner 1980, Angel and Baker 1982, Smith 1982, McCave 1983, Angel 1990). Particles available for consumption include large particles and their associated microbial communities that have sunk rapidly from shallower or surface waters (e.g. Silver and Alldredge 1981, Gowing and Silver 1985, Silver and Gowing 1991, Turley 1991), smaller suspended particles and organisms (e.g. reviewed by Vinogradov and Tseitlin 1983, Silver et al. 1986, Karl et al. 1988, Wakeham and Canuel 1988), and particles and organisms living on the sea floor (e.g. Burnett 1981) that could be resuspended. The quantity and quality of carbon in the various particles is likely to differ among particle type and with depth.

Mid-ocean seamounts provide the ideal environment to compare the feeding ecology of benthic boundary-layer zooplankton at several depths, because upper water-column processes are relatively similar across a steep bathymetric gradient. Volcano 7, an inactive seamount in the eastern tropical Pacific Ocean, at 13° 23'N; 102° 27'W (Batiza 1980), provided such a site for this study. The biology of this seamount has been described by Wishner et al. (1990) and by Levin et al. (1991), and is summarized here. The summit of the seamount lies at 730 m depth and penetrates into the pronounced regional oxygen-minimum zone. The presence of abundant detrital material visible on the seamount summit and the high organic carbon content (including chlorophyll *a*) of the sediment suggest that much undegraded material reaches the seamount from the overlying water column. We hypothesized that particles sinking out of the euphotic zone (base at 85 m) immediately enter the broad oxygen-minimum zone (extending from ~70 to 1300 m depth), through which they transit relatively unaltered because of the reduced numbers of metazoan consumers. The sum-

mit of the seamount appears to be a benthic faunal transition zone related to the oxygen gradient at the lower interface of the oxygen-minimum zone. Abundances of benthic macrofauna and megafauna are low on the upper summit (~730 to 750 m), probably because of the physiological limitations of low oxygen, but peak dramatically tens of meters deeper on the lower summit (peak at about 800 m), where oxygen content is slightly higher. The abundance gradient of sediment bacteria and meiofauna is the reverse of that of macrofauna, with highest values on the upper summit. The flank (1300 m) and base (3400 m) of the seamount have a more normal deep-sea benthic fauna, and there is evidence for the winnowing of fine particles from the flank by currents and the deposition of these particles at the base. Near-bottom zooplankton may show trophic responses to some of these habitat features.

The purpose of our study was to determine the feeding ecology of particle-feeding benthic boundary-layer zooplankton. We focused on copepods as the dominant metazoan zooplankton, and on phaeodarian radiolarians as large (800 μm to 2 mm) particle-feeding protozooplankton. We present the first data comparing gut and vacuole contents of selected organisms at four depths to suspended, resuspended, and sinking particles in the environment, and show that specific gut contents can indicate the types of particles consumed by detrital feeders.

Materials and methods

Sample collection

Zooplankton for gut-content analysis were collected at Volcano 7 from 23 November–4 December 1988, in the benthic boundary layer at ~1 to 5 m above the bottom at four sites: the upper summit (724 to 770 m), the lower summit (769 to 888 m), the flank (1278 to 1339 m), and the base (2969 to 3112 m). Collections were made from the D.S.R.V. "Alvin", with plankton tows (183 μm mesh) of approximately 1 h duration, using a multiple sampling opening-closing net system with closing cod ends and a recording flow meter (Gowing and Wishner 1986, Wishner and Gowing 1987). Plankton was preserved in situ with glutaraldehyde. Some animals were also used from shorter (~10 min) tows that had been terminated with the injection of m-aminobenzoic acid ethyl-ester methanosulfanate salt (MS-222) (Wishner and Meise-Munns 1984). Organisms from the latter tows were preserved with formaldehyde within 1 h of their return to the ship.

Multitrap particle-interceptor traps (Knauer et al. 1979) were deployed for ~3 d at 8 m above the sea floor at the lower summit (792 m), flank (1282 m), and base (2962 m). Current meters placed at 4.5 m above the sea floor recorded the magnitude of currents during the trap deployment. At each site, six replicate collecting tubes for microscopical analysis contained formaldehyde in a sucrose density-gradient solution (Gowing and Silver 1983), and six tubes for carbon, hydrogen, and nitrogen (CHN) analysis contained formaldehyde in a salt solution (Knauer et al. 1979). Contents of tubes for microscopy were stored in the dark in glass bottles until analysis. Contents of tubes for CHN analysis were filtered at sea onto either pre-weighed 0.8 μm, 47 mm-diam Nuclepore filters or pre-combusted 47 mm glass-fiber filters. Large copepods were removed from the filters with forceps. Filters were dried in a 60 °C oven for 12 to 24 h and stored in a desiccator until analysis.

Two 4-liter water samples were collected and preserved in situ on each dive at each site using marine-snow samplers (Gowing and Wishner 1986) that had been newly modified by the placement of the 50% glutaraldehyde fixative in syringes; the syringe plunger was shortened and attached to the outside of the tube with monofilament line. The rubber on the plunger was filed so that it just sealed the syringe; the closure of the tube pulled the plunger out of the syringe and allowed release of the fixative. After removal of a 100 ml aliquot for bacterial counts from each sample, one sample was gravity-filtered onto a 3 μm Nuclepore filter at sea and the filter placed in a vial of buffered paraformaldehyde. The other sample was stored under refrigeration in a glass bottle until microscopical examination.

Aliquots of sediment samples and xenophyophores (phylum Sarcomastigophora, class Xenophyophorea) collected with box or tube corers as described by Levin et al. (1991) were preserved with buffered paraformaldehyde after their return to the ship.

Microscopical analyses

Copepod species selected for gut-content analysis were relatively abundant (several specimens in a sample) and easily identified, and included individuals with apparent gut contents, as evaluated by light microscopy. Phaeodarian radiolarians selected for vacuole-content analysis were relatively abundant, and individuals were chosen because of their large and dense phaeodia. Copepods were prepared for transmission, electron microscope (TEM) gut-content analysis using the methods of Gowing and Wishner (1986). Several mysids from the summit, a few amphipods, and an ostracod were similarly prepared. Phaeodarian radiolarians were prepared for TEM using the methods of Gowing (1986), and xenophyophores were first decalcified using the method of Houk and Hinegardner (1980) and then prepared for TEM using the methods for phaeodarians. Copepods were oriented longitudinally so that contents from the largest possible gut area could be recorded in thin sections. The posterior midgut was examined to reduce the possibility of analyzing gut contents resulting from feeding during the plankton net tow. Phaeodarian radiolarians were thin-sectioned to include as many vacuoles as possible in sections. Contents of 5 to 20 vacuoles were recorded for each specimen.

Replicate unfiltered water samples collected with the marine-snow samplers and replicate particle-interceptor trap samples were allowed to settle for several days, and then the supernatant solution was siphoned off, leaving a volume of a few hundred milliliters. Aliquots of this solution were settled in 50 or 100 ml settling chambers to which a few drops of a 1.0 mg ml^{-1} solution of the nuclear fluorochrome 4′, 6-diamidino-2-phenylindole, DAPI (Coleman 1980, Porter and Feig 1980) had been added. Entire samples were counted using an inverted compound microscope at 150× for protozoans, metazoans, and skeletal material >30 μm. Subsamples of the chambers were counted at 400× for smaller (≤30 μm) protozoans and minipellets (Gowing and Silver 1985). The presence of a stained nucleus was assumed to indicate that an organism had been alive at the time of capture (see Gowing 1986 for discussion). Crustacean "swimmers" and cryptic swimmers (Michaels et al. 1990) in particle-interceptor trap samples were counted and measured so that their carbon content could be estimated and subtracted from the CHN values for the total trap contents (see subsection "Carbon measurements and conversions").

Aliquots of filtered water samples collected with the marine-snow samplers (material was gently squirted off the Nuclepore filters), particle-interceptor trap samples, and samples of the upper half centimeter of the sediment were prepared for examination with scanning electron microscopy (SEM) and for TEM using the methods of Gowing and Wishner (1986). Only the lighter material in the sediment surface layer (obtained by shaking the sample, letting it settle briefly, and then removing material still in suspension) was examined with TEM. Additional samples were prepared for SEM by settling on polylsine-coated coverslips that had been placed in settling chambers [modification of method of Marchant and Thomas (1983) by K.R. Buck, Monterey Bay Aquarium Research Institute, Monterey, California, personal communication]. It should be

noted that, because the samples for SEM and TEM are so small, the absence of a certain particle type does not mean that the particle type is not present in the environment. Mysid gut contents for SEM were prepared by dissecting the gut contents into a few drops of fixative, gently dissociating the contents with a probe, and then transferring this material to a 0.2 μm pore-size polycarbonate filter. The gut material on the filter was then processed as described for the water samples.

Elemental microanalysis was performed on two types of mysid gut-content samples, using a Princeton Gamma-Tech System 4 Energy Dispersive Spectrometer (EDS) system on an ISI WB-6 scanning electron microscope. Thick (~1.0 μm) sections of mysid gut contents embedded for TEM as described above (except that the postfixation with osmium was omitted) were dried onto carbon disks, coated with carbon, and examined. An x-ray spectrum was obtained from an area of ~52 μm^2 in the center of the gut, another spectrum was obtained from an equivalent area of the section outside the gut (a resin blank), and the latter was subtracted from the former. X-ray spectra were similarly obtained for SEM preparations of mysid gut contents (described in the previous paragraph), using an area of the Nuclepore filter with no gut contents as a blank.

Bacteria in water and trap samples were counted using the method of Parsons et al. (1984), except that two drops of a 1.0 mg ml^{-1} solution of DAPI were used instead of acridine orange to stain the bacteria. Two hundred to 500 cells were counted from each sample. Because these samples were counted after storage (refrigerated in the dark) for 2 yr, the abundances should be considered minimal estimates (Spinrad et al. 1989, Turley and Hughes 1992). We are assuming that the abundances are valid for comparison among sites, but we have no data to indicate that this is true.

Carbon measurements and conversions

CHN measurements were made on suspended and trapped particulates and groups of large (800 μm to 2 mm diam) phaeodarian radiolarians using a Carlo Erba 1106 Elemental Analyzer. Aliquots (100 to 150 ml) of water samples were gravity-filtered through acid-cleaned syringes onto pre-combusted 13 mm-diam Whatman GF/F glass-fiber filters. Filters were dried at 60 °C and stored in a desiccator until analysis. Two filter blanks for each dive or hydrocast were prepared by following all procedures for samples except that no water was filtered, and mean values of the blanks were subtracted from values for the samples. Two replicates of each sample were analyzed; a third replicate was analyzed if the first two differed significantly. Glass-fiber filters containing filtered trap samples were cut into 12 pie-slice shaped pieces and analyzed separately because whole filters were too large for analysis. The CHN values of each slice were summed to obtain total carbon and nitrogen values. Trap samples filtered onto pre-weighed Nuclepore filters were weighed on a Cahn Model 4700 automatic electrobalance after placement in a 60 °C oven overnight. The material on the filters was then subsampled for carbon and nitrogen analysis. Subsamples were removed by scraping the filter surface gently with acetone-cleaned Teflon and stainless steel forceps. Phaeodarians were picked live from cod-end bottles, rinsed in deionized water, and placed on pre-cleaned, pre-weighed tin disks. Samples were dried in a 60 °C oven overnight and stored in a desiccator until analysis. Before analysis, disks were placed in a 60 °C oven overnight and weighed on a Cahn electrobalance.

Carbon content of protozoans previously counted and measured in the water and trap samples was calculated from volumes using the conversion: pg carbon = 0.08 × (volume in μm^3); Beers and Stewart 1971). A mean value of 33 ± 32 μg C per phaeodarian (N=23) from the CHN analyses was used for the large phaeodarians. Carbon content of cryptic metazoans and of metazoans that would not have been removed with forceps (e.g. small crustaceans) from the filters for CHN analysis was calculated from trap samples for microscopy using the method of Michaels et al. (1990). This metazoan "swimmer" carbon was subtracted from total carbon measured from the CHN replicate samples.

Statistical analysis

Abundance and carbon values were compared among the sites using a Kruskal-Wallis non-parametric analysis of variance (SAS Institute, Inc. 1988) or the r_sP_c statistic, where r_s is Spearman's rank correlation and P_c is the complement of the P-value (Rice and Gaines 1992). This statistic allows testing of alternative hypotheses where the order of class (i.e., sites, in the present data set) values is predicted. Mann-Whitney U-tests were subsequently used for pairwise comparisons of sites, using a modified Bonferroni technique (Holm 1979 described by Rice 1989) to calculate a table-wide alpha level.

Results

Gut contents of zooplankton

Copepods represented a mean of 82 ± 10% (range 57 to 95%; N=40) of the zooplankton by number. Gut contents were recorded for 43 specimens of 12 species or groups of calanoid copepods from the summit, for 26 specimens of 7 species or groups from the flank, and for 10 specimens of 7 species or groups (including some non-calanoids) from the base (Table 1). The species from which the individuals were examined for gut-content analysis represented a mean of 18 ± 14% (range 0 to 57%; N = 39) of the total calanoid copepods in a sample. Gut contents could be classified into the following general categories: (1) predominantly bacteria-like bodies (Fig. 1 A–D), (2) predominantly detrital particles and associated cells, sometimes with small amounts of cuticle or digested tissue (Fig. 1 E), (3) predominantly digested tissue, sometimes with detrital particles embedded in it, and (4) what appeared to be cytoplasm that could have originated from the copepod's own gut epithelium (Nott et al. 1985).

We consulted several experts (see "Acknowledgements") about the bacteria-like bodies, and opinions about what they might be ranged from bacteria to some type of organelles or granules from an ingested organism. The size, shape, electron-density, and cell-wall ultrastructure (visible in a few specimens, e.g. Fig. 1 C) are most consistent with gram-positive bacteria (B. Finlay personal communication). The lack of obvious cell walls and internal structures (e.g. Fig. 1 D) in the majority of specimens could result from less than optimal fixation (the gut contents are fixed only after the aldehyde fixative penetrates the zooplankton) and or partial digestion by the zooplankton before fixation. We were not able to stain these bodies definitively with DAPI because the gut contents of the remaining (non-embedded) specimens did not contain enough of them. Because we could not use either the gram stain or DAPI, we will refer to these bodies as bacteria-like bodies. There were no large amounts of metals or unique elements in the resin sections or filter preparations. The x-ray spectrum resulting from the subtraction of the resin blank from the gut-content section showed small peaks of sodium, aluminium, sulfur, and calcium, and slightly larger peaks of chlorine and potassium. The x-ray spectrum resulting from the subtraction of the filter blank from the gut contents on

Table 1. Gut and vacuole contents of zooplankton collected from Volcano 7. Sites: US, upper summit of seamount, depth range 731 to 752 m ($N=2$); LS, lower summit, depth range 775 to 880 m ($N=11$); F, flank, depth range 1259 to 1332 m ($N=14$); B, base, depth range 2945 to 3100 m ($N=13$). Sex: f, female, m, male, i, immature. Abund.: abundances (nos. 1000 m^{-3}), calculated from forty 10-min tows; because samples were small and variable, a single abundance was calculated from sum of counts from all cod-ends, divided by total volume filtered; for *Lucicutia* aff. *L. grandis*, total abundance for females, males, and immatures is given; na: not available because species did not occur in feeding bottles or was combined with another species. Sec.: number sectioned. Guts: no., number with gut contents; (type), type of gut contents (C = crustacean cuticle, E = copepod gut epithelium, P = detrital particles and

Species	Site	Sex	Abund.	Sec.	Guts		Gut/vacuole contents:				
					no.	(type)	Bacteria-like bodies, bacterial cells, and remnants				
							Blb	Bac	Mpb	Mpc	Cya
Metazoans											
Eucalanus inermis	US	f	8105.5	3	3	(2T, 1E)	0	0	0	0	0
Heterostylites longicornis	US	f, m	1537.4	3	3	(3P)	33	100	0	0	0
Lucicutia aff. *L. grandis*	US	f	3007.3	1	1	(1TP)	0	100	0	0	0
Lucicutia aff. *L. grandis*	US	i, m		4	4	(2P, 2PT)	75	25	0	0	0
Bradyidius sp.	LS	f	44.1	6	2	(2P)	0	100	50	100	0
Euchirella sp.	LS	f	82.3	5	1	(1E)	0	0	0	0	0
Gaidius pungens	LS	i	58.2	5	4	(3P, 1PC)	50	100	25	25	0
Pleuromamma robusta	LS	f	453.9	8	8	(6T, 2TP)	0	0	0	0	0
Undinella sp. V1	LS	f, m	94.3	9	5	(3TP, 2T)	0	0	0	0	0
Scaphocalanus sp.	LS	f	na	1	0						
Scaphocalauns major	LS	f	9.5	2	2	(2PT)	0	100	0	0	50
Scaphocalanus spp.	LS	i	21.5	4	3	(2P, 1TP)	33	33	0	0	33
Xanthocalanus spp.	LS	i	241.5	7	7	(6P, 1T)	43	57	0	0	0
Euchirella sp.	F	f	47.5	2	0						
Gaidius pungens	F	i, f	57.2	4	4	(4P)	25	50	0	0	0
Undinella sp. V2	F	i, f	33.0	6	6	(4TP, 2T)	0	17	0	0	0
Scaphocalanus? sp.	F	m	na	2	2	(2P)	100	50	0	0	0
Scolecithricella sp.	F	i, f, m	31.3	13	12	(7P, 1C, 2T, 2PT)	50	25	0	0	8
Temorites sp.	F	f	na	1	1	(1T)	100	0	0	0	0
Xanthocalanus spp.	F	i	34.8	2	1	(1P)	100	0	0	0	0
Aegisthus sp	B	?	18.0	1	1	(1P)	100	100	0	100	0
Benthomisophria sp.	B	?	20.9	1	1	(1T)	0	0	0	0	0
Cornucalanus? sp.	B	i	18.0	1	0						
Undinella sp. V2	B	?	189.1	8	5	(3TP, 2T)	20	0	0	20	0
Spinocalanus sp.	B	f	13.1	2	2	(1P, 1PC)	50	100	50	50	50
Xanthocalanus spp.	B	i	28.0	1	1	(1P)	100	100	0	0	0
Microsetella-like	B	?	79.5	1	1	(1P)	0	100	0	0	100
Boreomysis sp.	LS	?	588.8	9	9	(7P, 2PC)	89	11	0	0	0
Ostracod	LS	?	105.6	1	1	(1P)	0	100	0	0	0
Amphipods	F	?	18.5	3	2	(2P)	50	0	0	0	0
Phaeodarian radiolarians											
Aulacanthidae	LS	–	30.7	6	–	(6P)	67	83	0	0	17
Castanellidae	LS	–	12.6	2	–	(2P)	50	100	0	0	0
Aulacanthidae	F	–	22.7	11	–	(11P)	82	91	0	0	0
Castanellidae	F	–	9.4	3	–	(3P)	0	100	0	0	0
Aulacanthidae	B	–	12.2	8	–	(8P)	62	100	0	12	12

the filter showed small peaks of sodium, and chlorine, and slightly larger peaks of calcium and phosphorus. The differences between the two sample preparations could reflect differences in gut contents (there was some amorphous material between the bacteria-like bodies) or differences in sample preparation for SEM and TEM.

The bacteria-like bodies occurred in 32 guts, or 35% of the metazoan zooplankton that were sectioned that had gut contents. For particle-feeding copepods, the percentage containing bacteria-like bodies ranged from 43 to 100%, depending on the site (Table 2). At the lower summit, the bacteria-like bodies made up most of the gut contents of 1 specimen of *Scaphocalanus* spp. (of 3 specimens sectioned that had gut contents), 3 specimens of *Xanthocalanus* spp. (of 7 specimens), and 6 specimens of the mysid *Boreomysis* sp. (of 9 specimens) from the lower summit. At the flank they made up most of the gut contents of 1 specimen of *Gaidius pungens* (of 4 specimens sectioned that had gut contents), 2 specimens of *Scaphocalanus*? sp. (of 2 specimens), 4 specimens of *Scolecithricella* sp. (of 12 specimens), 1 specimen of *Xanthocalanus* spp. (the only one with gut contents), and 1 amphipod (of 2 specimens). At the base they made up most of the gut contents of 1 specimen of *Xanthocalanus* spp. (the only one with gut contents). These bodies were found in smaller numbers in a total of 12 other specimens,

cells, PT = particles with tissue, T = tissue, TP = tissue with particles), types are preceded by percentages of individuals with gut contents that contained the different contents. Gut/vacuole contens: Blb, bacteria-like bodies; Bac, bacteria (Blb and Bac were differentiated on basis of ultrastructure); Mpb, metal-precipitating bacteria; Mpc, capsule of metal-precipitating bacterium; Cya, cyanobacteria or prochlorophytes; Chl, *Chlorella*-like cell; Alg, other algal cell; Dia, diatom; Sca, algal scales; Slf, silicoflagellate skeleton; Pzn, protozoan; Flg, flagellate; Lor, tintinnid lorica; Coc, coccolith; For, foraminiferan test; Nem, cnidarian nematocyst; Cut, crustacean cuticle; Tis, amorphous tissue-like material; Ogm, olive-green material; Ogb, olive-green body/minipellet; Sil, siliceous fragment; Amp, amorphous material. –: not applicable to phaeodarians

Gut/vacuole contents:

Algal cells and remnants					Protozoan cells and remnants					Metazoan remains			Detrital and amorphous materials			
Chl	Alg	Dia	Sca	Slf	Pzn	Flg	Lor	Coc	For	Nem	Cut	Tis	Ogm	Ogb	Sil	Amp
0	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0
0	66	0	33	0	33	0	67	0	0	0	100	0	67	100	67	33
0	100	0	0	0	100	0	100	0	100	100	100	0	0	100	100	0
25	0	0	0		0	0	0	0	0	25	25	0	25	75	75	50
0	0	100	50	50	50	50	0	0	0	0	0	0	100	100	100	100
0	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0
50	75	50	0	0	0	0	50	0	0	50	75	0	100	100	100	50
0	12	0	0	0	0	0	0	0	0	0	0	75	25	0	0	25
0	0	0	0	0	0	0	0	0	40	20	100	0	40	20	0	0
100	100	50	0	0	0	0	0	50	0	0	50	50	100	50	100	50
33	33	33	0	0	0	0	0	0	0	0	33	0	100	33	67	100
0	14	14	14	0	0	0	0	14	0	14	42	14	42	14	71	28
25	25	25	0	0	0	0	25	0	0	25	50	25	100	75	100	75
0	0	17	0	17	0	0	0	0	0	67	0	100	67	33	50	17
0	50	0	0	0	0	0	0	0	0	0	50	0	50	0	100	50
17	25	17	0	8	0	0	0	0	0	17	25	17	50	25	50	50
0	0	0	0	0	0	0	0	0	0	0	0	100	0	100	0	100
0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0	100
0	0	100	0	0	0	0	0	100	0	0	0	0	100	0	100	100
0	0	0	0	0	0	0	0	0	0	100	0	100	100	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	80	0	20	20	0
50	50	50	0	0	0	0	0	50	50	0	100	0	100	100	100	100
0	0	0	0	0	0	0	0	100	0	0	0	0	100	0	0	0
100	100	100	0	0	0	0	0	0	0	0	0	0	100	100	100	0
11	11	11	0	11	0	0	0	33	0	11	56	22	22	22	22	56
0	0	100	0	0	0	0	0	0	0	0	0	0	100	100	100	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0
33	67	0	0	0	0	0	17	17	0	0	50	0	100	–	50	100
0	50	50	0	0	0	0	50	0	0	0	0	0	50	–	50	100
42	50	0	10	0	0	0	0	0	0	0	36	18	91	–	82	100
67	100	0	0	0	0	0	0	0	0	0	33	0	33	–	100	100
62	25	12	12	0	0	0	0	0	0	0	0	12	100	–	62	100

as shown in Table 1. The bacteria-like bodies also occurred in vacuoles of 19 of the phaeodarian radiolarians, or 63% of the specimens sectioned.

Detrital particles in the guts included olive-green "cells" or "bodies" (e.g. Fournier 1970, Silver and Bruland 1981) or minipellets (Gowing and Silver 1985) (Fig. 1D), olive-green material (material visually similar to the content of the former particles but not in discrete packages), tintinnid lorica material, fragments of siliceous and calcareous plankton, and "amorphous" material that could not be identified even with TEM. As discussed previously (Gowing and Wishner 1986), "amorphous" material could be cytoplasm or detrital material digested beyond recognition. Detritus of metazoan origin included occasional pieces of cuticle and cnidarian nematocyst walls. Material of algal origin included *Chlorella*-like cells, other small cells with chloroplasts (Fig. 2A), cells with lamellae, and polyhedral bodies that could be either cyanobacteria or prochlorophytes (Fig. 2B) (Chisholm et al. 1988), diatoms with cytoplasm, and scales of prasinophytes. A few heterotrophic protozoans and remnant scales were observed. Bacteria recognizable as such with TEM but with no distinctive morphology, metal-precipitating bacteria (Fig. 2C), and empty capsules of metal-precipitating bacteria also occurred. No evidence of gut bacteria attached to the gut

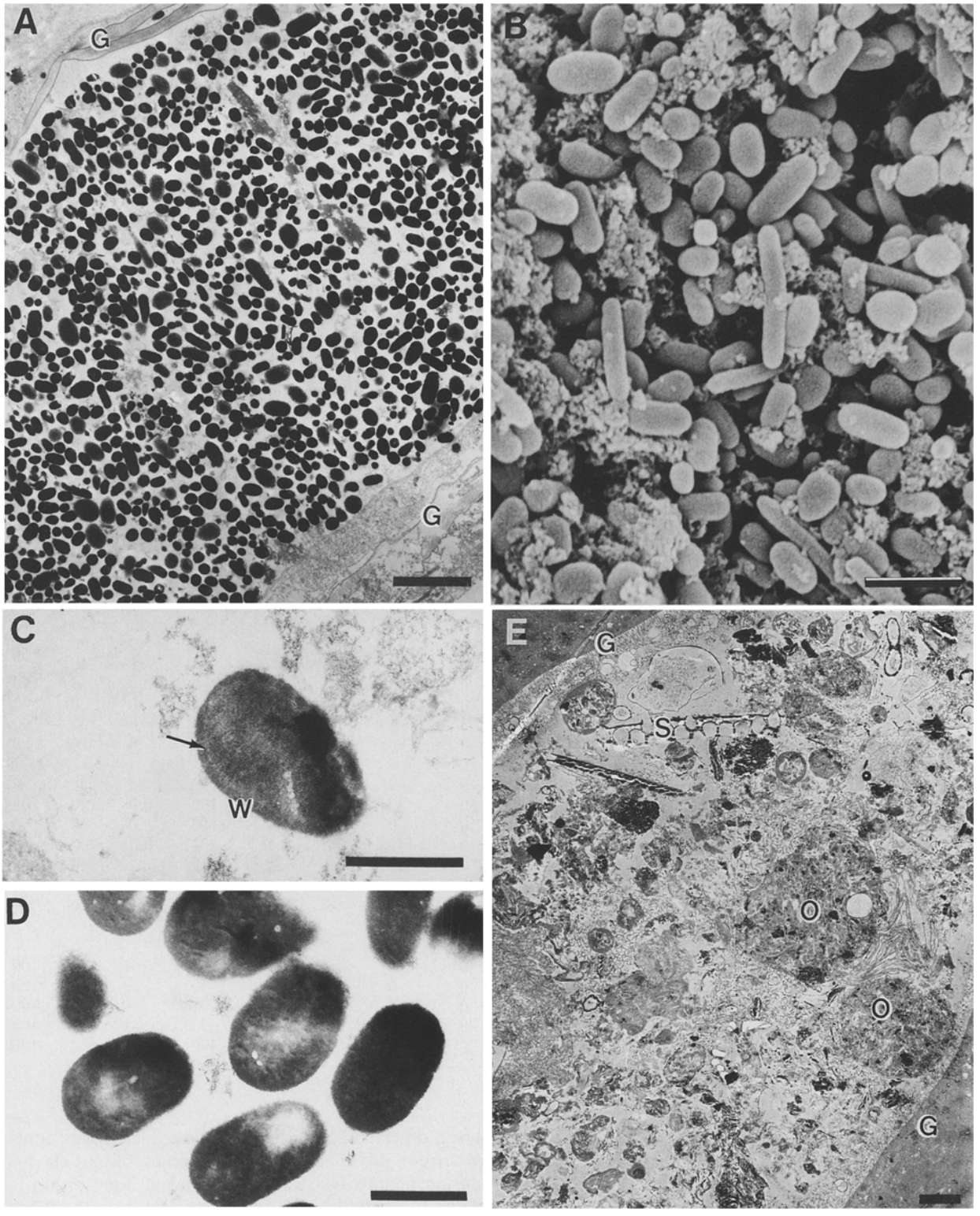

Fig. 1. Gut contents of zooplankton. (A) Longitudinal section through gut of the copepod *Xanthocalanus* sp. from lower summit of tropical Pacific seamount Volcano 7; dark spots are bacteria-like bodies; G: gut wall (scale bar = 2.0 μm). (B) Scanning electron micrograph of bacteria-like bodies from gut of mysid *Boreomysis* sp. from lower summit (scale bar = 1.0 μm). (C) Bacteria-like body; white line marked by the arrow shows location of cell membrane separating cell wall (W) from rest of cell; this ultrastructure is characteristic of gram-positive bacteria (scale bar = 0.5 μm). (D) Bacteria-like bodies with no obvious ultrastructure (scale bar = 0.05 μm). (E) Longitudinal section through gut of copepod *Bradyidius* sp. from upper summit; contents are typical of gut of a detritivore, and include olive-green bodies or minipellets (O) surrounded by olive-green or detrital material with occasional siliceous fragments (S); G: gut wall (scale bar = 1.0 μm)

Table 2. Percentage of particle-feeding individuals containing specific cells and particles at three sites on seamount. (*N*): number of specimens

Contents	Summit	Flank	Base
Copepods	(23)	(17)	(4)
detrital particles	91	71	100
amorphous material	57	59	75
olive-green bodies	65	41	50
algal cells	65	41	50
bacteria	70	30	100
bacteria-like bodies	43	59	100
Phaeodarians	(8)	(14)	(8)
detrital particles	100	100	100
amorphous material	100	100	100
cuticle	38	36	0
algal cells	63	79	63
bacteria	100	100	100
bacteria-like bodies	62	64	63

microvillar border were seen in any zooplankton specimens.

Three of the summit species (*Eucalanus inermis*, *Lucicutia* aff. *L. grandis*, and *Heterostylites longicornis*), were especially abundant at the upper summit oxygen-interface region. There were no pronounced differences in gut contents between copepods from the upper and lower summit. No specimens from the upper summit had guts packed with bacteria-like bodies, whereas some specimens from the lower summit did. However, the sample size from the upper summit was smaller, and the same species from the upper and lower summit were not analyzed. Small numbers of the bacteria-like bodies were, however, found in gut contents analyzed from upper-summit copepods. Generally, particle-feeding copepods and phaeodarian radiolarians had fed on similar particles at the three sites (Table 1).

Among the predominantly carnivorous copepods, gut contents indicative of metazoan prey included large amounts of crustacean cuticle and undigested nematocysts (Fig. 2D). Embedded in some of the prey tissue were particles such as olive-green bodies, olive-green material, silica fragments, and occasional algal and bacterial cells, indicating that the carnivores had consumed detritivores.

One specimen of *Eucalanus inermis* from the upper summit and one specimen of *Euchirella* sp. from the lower summit contained what appeared to be hindgut contents comprised of disintegrated gut epithelial cells similar to those described by Nott et al. (1985) for *Calanus helgolandicus*.

Occasional specimens that appeared to have gut contents when evaluated with light microscopy were found to have empty guts when sectioned. These can be determined from the data in Table 1 by subtracting the number of specimens with gut contents from the number sectioned.

Vacuole contents of phaeodarian radiolarians

Phaeodarians examined with TEM included members of the families Aulacanthidae and Castanellidae (Table 1). Vacuole contents included bacteria-like bodies (Fig. 2E), algal cells and remnants such as cyanobacteria or prochlorophytes, *Chlorella*-like cells, other small algal cells, diatoms, and algal scales. Bacteria with non-distinctive internal morphology were common. No metal-precipitating bacteria were observed, but two metal capsules were recorded. Amorphous material that could have been detritial in origin or possibly digested cytoplasm was common. Detrital material included olive-green material, tintinnid loricae, siliceous and calcareous fragments, and diatom frustules. Cuticle was the only material of metazoan origin observed.

Suspended organism and particles

Mean abundances of suspended protozoans ranged from 2×10^{-5} large phaeodarians l^{-1} at the base to 19 ciliates plus flagellates l^{-1} at the summit (Table 3). Mean protozoan biomass was generally less than 11 ng C l^{-1}. Abundance and biomass of ciliates and flagellates and abundance of large phaeodarians differed significantly among sites; abundance and biomass of sarcodines other than large phaeodarians differed significantly among sites; abundance and biomass of sarcodines other than large phaeodarians did not. Mean bacterial abundances, that should be considered minimum estimates, as discussed in last paragraph of "Material and methods – Microscopical analyses", ranged from 7.8×10^7 l^{-1} at the base to 2.0×10^8 l^{-1} at the summit, and were significantly lower at the base than at the other sites. Protozoan carbon made up 0.04, 0.02, and 0.01% of the total particulate organic carbon at the summit, flank, and base, respectively.

Mean abundances of suspended skeletal materials (radiolarian skeletons, foraminiferan tests, and tintinnid loricae) were generally less than 10/liter at the three sites (Table 3) and did not differ significantly among the three sites. Mean abundances of minipellets or olive-green bodies were significantly higher at the base than at the summit. Other siliceous and calcareous planktonic skeletal material observed with SEM included radiolarian and diatom test fragments making up siliceous debris, intact centric and pennate diatoms, coccoliths, thoracospheres, and silicoflagellates, and was generally similar at the three sites (Table 3). Amorphous and other detrital material and bacteria of various morphologies, including bacteria-like bodies, viewed with TEM, were also present (Table 3).

Sinking plus resuspended organisms and particles

Sinking plus resuspended organisms and particles collected in particle-interceptor traps are reported as "fluxes" (U m^{-2} d^{-1}); quotation marks are used because, conventionally, flux is a measurement of sinking particles where-

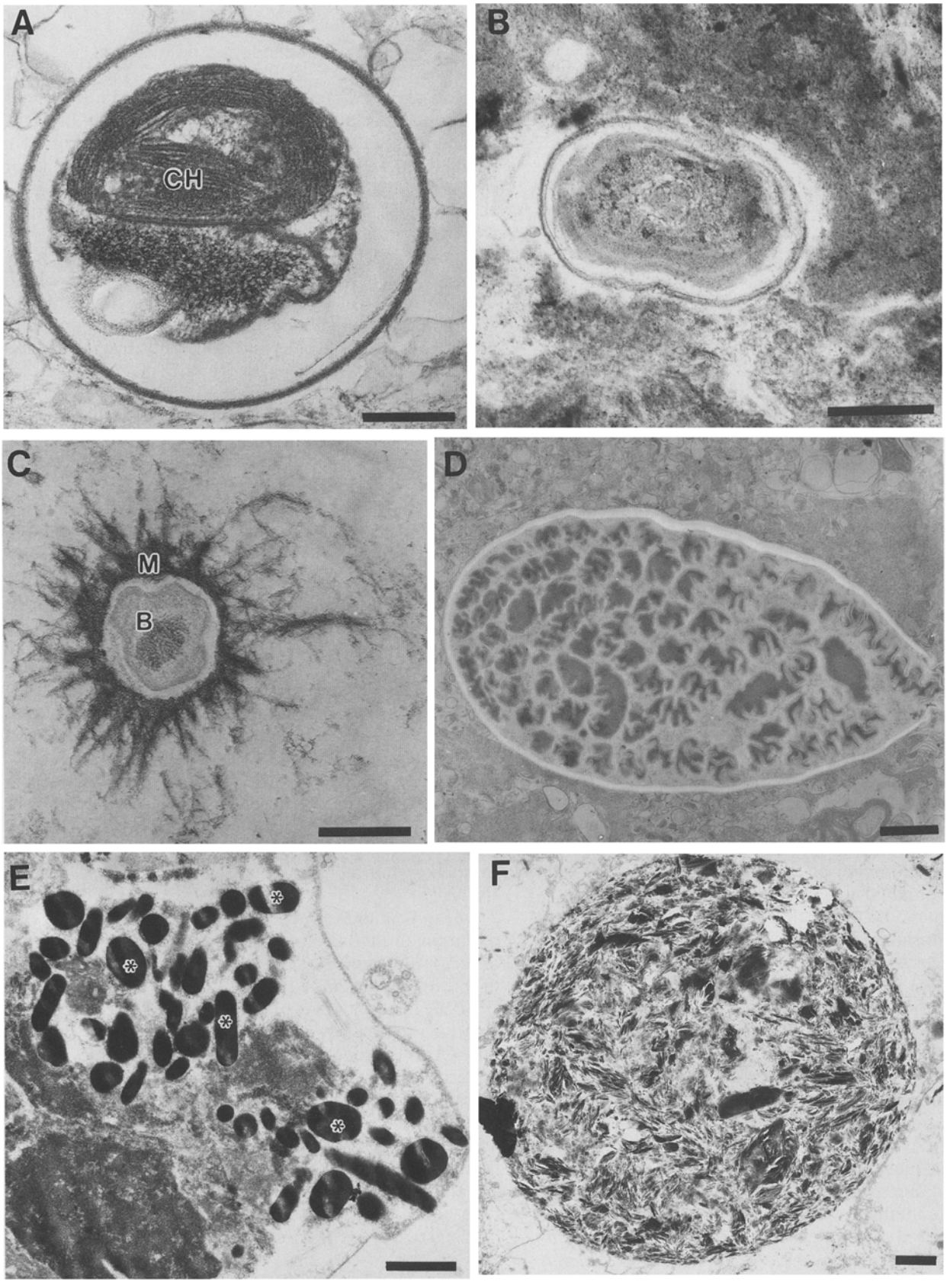

Fig. 2. TEMs of gut contents of zooplankton, contents of a phaeodarian vacuole, and a stercome (fecal pellet) of a xenophyophore. (A) Algal cell from gut of specimen of copepod *Lucicutia* aff. *L. grandis* from upper summit; CH: chloroplast (scale bar = 0.5 μm). (B) Cyanobacterium or prochlorophyte from gut of copepod *Spinocalanus* sp. from flank of seamount (scale bar = 0.5 μm). (C) Metal-precipitating bacterium from gut of copepod *Gaidius pungens* from lower summit; B: bacterial cell; M: metal capsule (scale bar = 0.5 μm). (D) Cnidarian nematocyst from gut of copepod *Undinella* sp. from the flank (scale bar = 1.0 μm). (E) Portion of feeding vacuole of a phaeodarian radiolarian of family Aulacanthidae from the flank; contents include several bacteria-like bodies (some marked with asterisks); (scale bar = 1.0 μm). (F) Stercome of xenophyophore from the flank; contents are detrital or "olive-green" material (scale bar = 1.0 μm)

Table 3. Suspended materials in water samples from Volcano 7. Mean abundances (nos. $l^{-1} \pm$SD) of organisms and carbon and mean carbon biomass (ng C $l^{-1} \pm$SD) of organisms. Other sarcodines include small (<800 μm diam) phaeodarian radiolarians, foraminiferans, acantharians, and the heliozoans *Sticholonche* spp. (*N*): number of samples analyzed. *P*: value for Kruskal-Wallis test or alpha value from table of critical values for $r_s P_c$ statistic, where r_s Spearman's rank correlation and P_c is complement of *P*-value (Rice and Gaines 1992); NS: not significant ($P > 0.05$); lettering in *P*-column denotes significant differences between pairs of sites, e.g. S > B indicates that value for summit was significantly higher than value for base. Material observed (+) and not observed (−) with SEM and with TEM is shown in bottom half of table

Material	Summit		Flank		Base		*P*
	734–818 m	(*N*)	1311–1343 m	(*N*)	2978–3150 m	(*N*)	
Organisms							
Large phaeodarian radiolarians							
abundance	$5 \times 10^{-5} \pm 6 \times 10^{-5}$	(27)	$3 \times 10^{-5} \pm 2 \times 10^{-5}$	(22)	$2 \times 10^{-5} \pm 3 \times 10^{-5}$	(21)	0.005,
biomass	1.65	(27)	0.99	(22)	0.66	(21)	S > B
Other sarcodines							
abundance	0.7±0.5	(5)	0.8±0.5	(3)	0.2±0.2	(3)	NS
biomass	11±16	(5)	3±3	(3)	0.3±0.5	(3)	NS
Ciliates and flagellates							
abundance	19±9	(5)	1.3±0.8	(3)	1.5±1.4	(3)	0.02
biomass	8.2±1.9	(5)	5.7±4.8	(3)	0.7±0.6	(3)	0.02
Bacteria							
abundance	$2.0 \times 10^8 \pm 8.8 \times 10^7$	(7)	$1.5 \times 10^8 \pm 4.3 \times 10^7$	(6)	$7.8 \times 10^7 \pm 6.4 \times 10^7$	(5)	0.0001, S, F > B
Total organic carbon	$55.3 \times 10^3 \pm 59.4 \times 10^3$	(6)	$39.0 \times 10^3 \pm 29.1 \times 10^3$	(6)	$18.9 \times 10^3 \pm 7.6 \times 10^3$	(3)	
Protozoan carbon	20.8		9.7		1.7		
Percentage of total that was protozoan	0.04%		0.02%		0.01%		
Particles							
Radiolarian skeletons							
abundance	3±4	(5)	5±4	(3)	6±6	(3)	NS
Foraminiferan tests							
abundance	4±3	(5)	56±47	(3)	3±3	(3)	NS
Tintinnid loricae							
abundance	0.4±0.2	(5)	0.2±0.1	(3)	0.4±0.2	(3)	NS
Minipellets							
abundance	$6.6 \times 10^3 \pm 6.4 \times 10^3$	(7)	$1.2 \times 10^4 \pm 3.6 \times 10^3$	(5)	$4.9 \times 10^4 \pm 3.6 \times 10^4$	(6)	0.01, B > S
SEM analysis							
Mineral debris	+		−		−		
Siliceous debris	+		+		+		
Coccoliths	+		+		+		
Diatoms	+		+		+		
Thoracospheres	+		+		+		
Silicoflagellate skeletons	+		+		+		
Sticholonche spines	−		−		+		
Choanoflagellate loricae	−		+		+		
Choanoflagellate cells	−		−		+		
Amorphous material	+		−		+		
TEM analysis							
Olive-green material	+		+		+		
Amorphous material	+		+		+		
Bacteria	+		+		+		
Metal-precipitating bacteria	+		+		+		
Capsules of metal-precipitating bacteria	+		+		+		
Bacteria-like bodies	+		−		−		
Cyanobacteria	−		+		−		

Table 4. Sinking plus resuspended material collected in particle-interceptor traps. Mean numerical "fluxes" (±SD) as nos. $m^{-2} d^{-1}$ of particles and organisms at three depths; (*N*): number of trap samples analyzed. Bacterial numerical fluxes are minimal estimates because of length of storage of samples before counting. Further details as in legend to Table 3

Material	Summit		Flank		Base		*P*
	792 m	(*N*)	1282 m	(*N*)	2962 m	(*N*)	
Organisms							
Acantharia	207±199	(5)	161±123	(6)	504±356	(6)	NS
Radiolaria	540±136	(5)	708±295	(6)	730±400	(6)	NS
Heliozoa	121±78	(5)	80±68	(6)	13±32	(6)	0.04
Foraminifera	104±145	(5)	121±144	(6)	63±77	(6)	NS
Ciliates >30 µm	7122±3012	(5)	6225±1936	(6)	4650±1654	(6)	0.04
Dinoflagellates >30 µm	3732±1107	(5)	2487±1493	(6)	5754±2199	(6)	0.02
Protozoans ≤30 µm	$4.1\times10^5\pm1.7\times10^5$	(4)	$7.6\times10^5\pm5.7\times10^4$	(6)	$4.8\times10^5\pm6.2\times10^4$	(3)	0.02
Diatoms	63±95	(5)	68±129	(6)	0	(6)	NS
Bacteria	$3.4\times10^9\pm8.3\times10^8$	(4)	$6.8\times10^8\pm2.8\times10^8$	(3)	$3.7\times10^9\pm1.9\times10^9$	(3)	NS
Particles							
Radiolarian skeletons	14896±3737	(5)	11619±2249	(6)	11158±5709	(6)	0.02
Foraminiferan tests	11672±4068	(5)	10066±2870	(6)	9439±2811	(6)	NS
Tintinnid loricae	2176±406	(5)	1182±699	(6)	995±426	(6)	0.01
Large fecal pellets (>50 µm)	3948±547	(5)	2569±1466	(6)	3599±786	(6)	NS
Minipellets (3–50 µm)	$3.8\pm10^6\pm1.4\times10^6$	(3)	$2.4\times10^6\pm4.4\times10^5$	(2)	$1.3\times10^6\pm1.1\times10^5$	(2)	0.01
SEM analysis							
Siliceous debris	+		+		+		
Diatoms	+		+		+		
Silicoflagellate skeletons	+		+		+		
Coccospheres	+		+		+		
Coccoliths	+		+		+		
Thoracospheres	+		+		+		
Sticholonche spines	+		+		+		
Choanoflagellate loricae ±cells	+		+		−		
Pollen	−		−		+		
TEM analysis							
Olive green bodies and material	+		+		+		
Amorphous material	+		−		−		
Bacteria	+		+		+		
Bacteria-like bodies	−		+		−		
Metal-precipitating bacteria	+		+		−		
Capsules of metal-precipitating bacteria	+		+		+		
Chorella-like cells	−		+		+		
Other algal cells	−		+		+		

as our values undoubtedly included naturally resuspended materials since the traps were so close to the sea floor. (Fluxes of living radiolarians, acantharians, foraminiferans, and the heliozoans *Sticholonche* spp. are all sinking fluxes because these organisms are all planktonic; the few benthic foraminiferans trapped did not contain cytoplasm.) Among living cells, numerical "fluxes" of acantharians, radiolarians, ciliates >30 µm, foraminiferans, diatoms, and bacteria were similar at the three sites (Table 4). "Fluxes" of the heliozoans *Sticholonche* spp., of ciliates and dinoflagellates >30 µm in longest dimension, and of protozoans ≤30 µm were significantly different among the sites. Among skeletal materials and fecal pellets, numerical "fluxes" of radiolarian skeletons, tintinnid loricae, and minipellets or olive-green bodies differed significantly among the three sites. Siliceous and calcareous skeletons and debris observed with SEM included silicoflagellate skeletons, coccospheres and coccoliths, thoracospheres, and siliceous debris including diatom fragments and *Sticholonche* spines, and were generally similar at the three sites (Table 4). Choanoflagellates of the species *Stephanoeca diplocostata* var. *paucicostata* and colonies of *S. cupola* (K. Buck, Monterey Bay Aquarium Research Institute, Monterey, California, and H. Thomsen, Institute for Sporeplanter, Copenhagen, Denmark, personal communication) were observed in material from the flank. TEM examiniation showed that trapped material from the three sites included bacteria (including bacteria-like bodies) and small algal cells (Table 4).

Carbon "fluxes" of acantharians, foraminiferans, dinoflagellates and ciliates >30 µm, and protozoans

Table 5. Organic carbon "fluxes" (mean ± SD) as mg C m^{-2} d^{-1} of components of trap material. Total "fluxes" are totals after subtraction of carbon from zooplankton "swimmers" (organisms believed to have entered traps without association with sinking particulates). Contents of several traps were combined to measure total carbon "flux". Further details as in legend to Table 3

Material	Summit, 792 m	Flank, 1282 m	Base, 2962 m	*P*
Organisms				
Acantharia	0.009 ± 0.008	0.021 ± 0.045	0.022 ± 0.023	NS
Radiolaria	0.039 ± 0.067	0.026 ± 0.024	0.310 ± 0.440	0.05
Foraminifera	< 0.001	< 0.001	0.002 ± 0.004	NS
Heliozoa	0.001 ± 0.004	< 0.001	0.001 ± 0.002	0.05
Dinoflagellates > 30 μm	0.044 ± 0.010	0.033 ± 0.018	0.071 ± 0.036	NS
Ciliates > 30 μm	0.019 ± 0.015	0.033 ± 0.022	0.013 ± 0.012	NS
Protozoans ≤ 30 μm	0.297 ± 0.180	0.190 ± 0.063	0.120 ± 0.050	NS
Total organic carbon	28	26	24.8	
Total protozoan carbon	0.409	0.303	0.539	
Percentage of total carbon that was protozoan	1.5%	1.2%	2.2%	

≤ 30 μm were similar at the three sites (Table 5). Carbon fluxes of radiolarians and the heliozoans *Sticholonche* spp. differed significantly among the sites. Carbon "fluxes" of the living protozoans made up 1.5% of the total organic carbon "flux" at the summit, 1.2% at the flank, and 2.2% at the base.

Although the traps were deployed for only 3 d at relatively great depths, numerous metazoan swimmers were trapped. In the aliquots counted from the six traps from the summit there were a total of 16 small copepods, 7 larvaceans, 3 ostracods, 6 pteropods, and 1 fragmented siphonophore. The six flank-trap aliquots contained a total of 21 small copepods, 4 larvaceans, 1 ostracod, 2 polychaetes, and three pteropods. The six base-trap aliquots contained a total of 43 small copepods, 1 amphipod, 2 chaetognaths, 1 jellyfish, 9 larvaceans, 12 ostracods, 1 polychaete, 4 pteropods, and 7 cnidarian tentacles. As discussed by Michaels et al. (1990), many of these organisms are invisible when viewed on white filters for CHN measurements of trap material; thus, we estimated their carbon content from counts and measurements of the samples for microscopy.

Overtrapping does not appear to have been significant at any site. Currents > 15 cm s^{-1} can cause particle-interceptor traps of our design to overtrap (Gardner 1980). Currents at the summit were < 10 cm s^{-1}, currents at the flank reached 17 cm s^{-1} but only for 7% of the deployment time, and current speeds at the base were < 5 cm s^{-1} (Levin et al. 1991).

Table 6. Qualitative SEM and TEM analysis of aliquots of the light material from uppermost 0.5 cm of three tube cores from summit region and two tube cores from flank and base regions. +: observed; −: not observed. "Mineral" particles are small angular particles whose origin cannot be determined from their morphology alone

Material	Summit, 746, 807, 857 m	Flank, 1320 m	Base, 2978, 3118 m
SEM data			
Intact skeletal material			
Diatoms	+	+	+
Coccospheres	+	−	−
Silicoflagellates	+	+	+
Radiolarians	+	+	−
Foraminiferans	+	+	−
Thoracospheres	+	−	−
Skeletal fragments			
Coccoliths	+	+	−
"Mineral" particles	+	+	−
Siliceous particles	+	+	+
Amorphous particles	−	−	+
Minipellets	+	−	+
TEM data			
Bacteria	+	+	+
Bacteria-like bodies	+	+	−
Metal-precipitating bacteria	+	+	+
Minipellets with bacteria-like bodies	+	−	−
Minipellets with refractory contents	+	+	−

Sediment

Many of the same types of materials and organisms present in the water were present in the upper 0.5 cm of the sediment surface. SEM examination showed the presence of diatoms, coccospheres, silicoflagellates, radiolarians, foraminiferans, thoracospheres, coccoliths and minipellets at the summit (Table 6). Diatoms, silicoflagellates, radiolarians, foraminiferans, coccoliths, mineral particles, and siliceous particles including diatom, silicoflagellate and radiolarian fragments were present at the flank site. Particulate material from the base sediment included diatom frustules, silicoflagellates, siliceous debris including radiolarian fragments, amorphous material and minipellets. TEM analysis of aliquots of the lighter material from the same samples revealed bacteria of various morphologies (including bacteria-like bodies) and minipellets with various contents (Table 6).

Discussion and conclusions

Zooplankton feeding ecology

The occurrence of large numbers of bacteria-like bodies in the guts of a variety of zooplankton is surprising. To our knowledge they have not been reported before, although reexaminiation of micrographs of copepod gut contents from the Santa Catalina Basin (Gowing and Wishner 1986) showed that small numbers of them were present in two specimens of *Xanthocalanus* spp. and in four small calanoids of 23 copepods analyzed. These bodies could be an enteric flora or remnants of food. At present the latter explanation seems more plausible, because they occurred in a variety of organisms but not in all specimens of specific organisms or species. They were also present in a variety of samples from the environmental: suspended particulates, "flux", sediments, and in phaeodarian vacuoles. Bacteria-like bodies in the environment could have come from a common source, and could have also been released as fecal pellets from the zooplankton that fed on the original source.

It is possible that the bacteria-like bodies could be organelles or granules of an ingested prey item. For example, the spherical cross-sections of the bodies resemble text book illustrations of zymogen or glycogen granules (e.g. Fig. 5 in Wagener and Pfennig 1987), and some of the ovoid or rod-shaped cross sections resemble amylopecten granules (e.g. Plate 1 b in Yarlett et al. 1981). The bodies are within the size range of melanosomes (Wilson 1981) and resemble electron micrographs of them (e.g. Fig. 1 in Epp and Frost 1985). The presence of sulfur and calcium are consistent with melanosomes, but melanosomes also contain iron (Wilson 1981). However, if the zooplankton had ingested another organism or several organisms, we should also have seen additional cellular remnants of the organisms. It was not possible to look at more anterior sections of the guts of these organisms to see if there were earlier stages of digestion present. Thus, the simplest explanation of the bacteria-like bodies is that they were free-living bacteria.

We hypothesize that the source of the bacteria-like bodies is a bacterial mat formed within the oxygen minimum or at its lower or upper interface. Formation of this mat at the upper interface is suggested by our finding of the bacteria-like bodies in a vacuole of a phaeodarian radiolarian from a surface plankton tow in the upper 50 m. An origin in a low-oxygen environment is consistent with occurrence of the bacteria-like bodies in guts of zooplankton from the Santa Catalina Basin. Near-bottom oxygen values there, while not as low as at Volcano 7, are as low as 0.3 ml l^{-1} (Smith et al. 1987). Bacterial mats have been reported from the oxic/anoxic interface in the water column of a tropical lake (Burnett et al. 1989), but to our knowledge such mats have not been reported from the open ocean. The hypothesized bacterial mats appear to be an important food item for particle-feeding zooplankton from the benthic boundary-layer because 43 to 100% of the organisms sectioned that had gut contents had ingested the bacteria-like bodies at the time of our sampling at Volcano 7.

The finding of gut contents consisting entirely of bacteria-like bodies suggests that several groups and species of zooplankton will consume a large aggregate of potential food if they encounter it. In most deep-sea environments such aggregates are not common, and thus gut contents normally reflect generalist feeding. The other detritivores from Volcano 7 and all the detritivores from the Santa Catalina Basin (Gowing and Wishner 1986) were generalists. Reports of gut contents consisting of only one type of organism or particle in deep-sea detritivorous zooplankton are uncommon in the literature. Chindonova (1959) described a specimen of the tropical mysid *Boreomysis spinifera* whose pyloric stomach was filled with bacterial spores. Interestingly, spore formation is a characteristic of gram-positive bacteria. Harding (1974) reported one specimen of the copepod *Ammalothrix emarginata* from 1000 to 2000 m in the Sargasso Sea that had eaten a large number of bacteria that appeared to be asssociated with a "detrital ball". These two cases are unusual.

Yet unanswered questions about detritivorous or omnivorous zooplankton in the deep sea are whether they can detect the quality of particles in a manner analogous to shallow-water copepods (e.g. Paffenhöfer and Van Sant 1985, Cowles et al. 1988, but see Reinfelder and Fisher 1991), and whether they preferentially ingest particles that are relatively undegraded. The presence of algal cells in copepod guts and phaeodarian vacuoles provides some circumstantial evidence for the latter. Furthermore, several algal cells were often found in a gut or vacuole; this is consistent with feeding on an aggregate with its accumulation of algal cells. Copepods and phaeodarians at the three sites had consumed small procaryotic and eucaryotic algal cells. Small algal cells in the deep sea originate from surface waters, and can reach the deep sea via several routes including aggregates and fecal pellets (reviewed by Silver et al. 1986). Recent studies have documented large amounts of phytodetritus from surface waters sinking rapidly to great depths (e.g. Lochte and Turley 1988, Thiel et al. 1988/1989). Algal cells with cytoplasm and nuclei occurred at the three sites in suspended and "flux" material. Although the presence of algal material was most pronounced at the summit, as shown by the high levels of chlorophyll *a* in surface sediments (Levin et al. 1991), algal cells reached the flank and base, as evidenced by their presence in particulate samples and in zooplankton guts and phaeodarian vacuoles. Evidence is accumulating for the feeding on sinking organic aggregates by deep-sea zooplankton in general. For example, Heffernan and Hopkins (1981, p. 461) reported "greenish brown detritus containing fragments of epipelagic microplankton" as common gut contents of the decapod *Bentheogennema intermedia* that lives below 900 m in the water column and does not undergo diel vertical migration. Studies on the actual contribution of these particles to the nutrition of these detritivores are needed now that the presence of such particles has been documented in guts of a wide variety of organisms.

The detrital particles (olive-green material, siliceous and calcareous debris) consumed by the particle-feeding copepods and by the phaeodarians were qualitatively

similar among individuals from the three sites. This material was abundant in guts and vacuoles. Siliceous material was more abundant than calcareous material in guts and vacuoles, although both types of material were common in the three environments. Whether this is a result of selective feeding on siliceous particles, avoidance of calcareous material, or digestive dissolution of calcareous material is not known. If copepods had ingested particulate material predominantly as olive-green bodies or minipellets (discussed in following paragraph), they would have ingested little if any calcareous material since we observed no calcareous material in these particles.

Olive-green cells (Fournier 1970), olive-green bodies (Silver and Bruland 1981) or minipellets (Gowing and Silver 1985) were common in copepod guts and were highest at the summit in suspended material and highest at the base in "flux" material. Olive-green bodies have several possible sources: resting cells of diatoms (Anderson 1975), senescent or digested algae (Silver and Bruland 1981), waste products of radiolarians (Gowing and Silver 1985), and stercomes (fecal pellets), of xenophyophores (Tendal 1972). They have previously been reported from guts of deep-sea copepods (Wheeler 1970, Harding 1974, Gowing and Wishner 1986). They resemble the waste vacuoles making up the phaeodarian radiolarians (Gowing and Silver 1985, Gowing and Wishner 1986), which were present at the three sites and in highest abundance at the summit. The dominant phaeodarians at the three sites were large (>800 μm) forms and nothing is known about their release of minipellets. Skeletons of large phaeodarians have been reported from deep-sea zooplankton guts (reviewed by Raymont 1983), but were not observed in guts in the present study. The olive-green bodies/minipellets in copepod guts were also morphologically similar to stercomes from xenophyophores at the flank and base (Fig. 2F). Xenophyophores made up 65.3% of the megafaunal organisms at the flank and 73.8% at the base (Levin et al. 1991). The contents of all the olive-green bodies/minipellets observed in copepod guts were predominantly amorphous and siliceous, with only occasional bacteria and rare algal cells. Some of the minipellets in phaeodarians contained abundant small algal cells, but no such minipellets were observed in copepod guts. Because the olive-green bodies/minipellets in the guts were morphologically similar to those with amorphous and siliceous contents observed in particulate material at the sites, in phaeodarian vacuoles, and in stercomes of xenophyophores, it was not possible to deduce the source of those the copepods had ingested.

We did not observe any dinoflagellate cells or remains in copepod guts or phaeodarian vacuoles. This is somewhat surprising because dinoflagellates (autotrophic and heterotrophic, thecate and athecate) were abundant in the particulate material. If they had been ingested, we should have observed them. They have been observed with light microscopy in copepod guts (e.g. Mullin 1966, Harding 1974, Hopkins 1985, 1987, Hopkins and Torres 1989), and their trichocysts can be recognized in phaeodarian vacuoles (e.g. Gowing 1989). At present the reason for their absence from the gut and vacuole samples examined is unknown.

Bacteria of various morphologies visualized with TEM (other than the bacteria-like bodies) were common in copepod guts and phaeodarian vacuoles, but there were no distinctive forms that could be traced to a certain environmental particle. Metal-precipitating bacteria and their capsules (Cowen and Silver 1984, Cowen and Bruland 1985) were present in copepod guts and in the different samples of particles from the environment at the three sites. Although we did not count these bacteria, they appeared to occur less frequently in guts of particle-feeding copepods at Volcano 7 than in the Santa Catalina Basin (Gowing and Wishner 1986, Wishner and Gowing 1992). Without counts of these bacteria from the environments, it would be difficult to interpret this finding. Metal-precipitating bacteria have been studied in hydrothermal vent plumes (Cowen et al. 1990, Cowen and Li 1991), but presently there is no hydrothermal activity at Volcano 7.

Zooplankton with empty guts are common in deep-sea samples (e.g. Harding 1974, Hopkins 1985), and may result from a variety of causes. For example, copepods may be in diapouase and thus not feeding. Many males do not feed. Several of the *Euchirella* sp. specimens had empty guts; this may have been because they were reproductive and were not feeding. Some female specimens of *Euchirella* sp. in summit and flank samples were carrying eggs, and there were many eggs loose in the samples. When feeding, copepods ingest discrete meals, so not all feeding copepods caught can be expected to contain gut contents. In our samples, there were occasional organisms with empty guts among species that had several members with gut contents. These organisms probably had not fed immediately before capture.

Comparison of particle consumption by copepods and phaeodarian radiolarians

Particle-feeding copepods and the large phaeodarian radiolarians consumed the same types of particles. Phaeodarians use pseudopodia to engulf particles, whereas copepods actively suspension-feed or capture particles. Both groups of organisms are predominantly generalists in that they had ingested a wide variety of particle types. Both groups had also ingested particles containing algal cells, indicative of a surface origin of the particle. These qualitative data suggest a similarity in feeding strategies between two very different groups of organisms in the same habitat. Furthermore, the particles ingested by both groups of particle-feeders at each depth were similar, suggesting that both groups select the same types of particles over a wide depth range.

Comparison with previous work on gut contents

In Table 7 we compare a summary of our feeding data for selected species and genera with data from the literature. With the exception of Gowing and Wishner (1986) who used TEM, previous researchers used light microscopy for gut analysis of deep-sea zooplankton. Both methods have advantages. Light microscopy allows one to view

Table 7. Trophic categories determined for zooplankton species and genera in present study compared to previous data from the literature. (No. spec): number of specimens with gut contents. Electron microscopy was used in present study and that of Gowing and Wishner (1986); the other studies used light microscopy

Species	Site	Depth (m)	(No. spec)	Trophic category	Source
Gaidius pungens	Volcano 7	775–880	(4)	detritivore	Present study
	NW Pacific	200–6000	(2)	omnivore	Chindonova (1959)
Lucicutia aff. *L. grandis*	Volcano 7	731–752	(5)	carnivore, detritivore, omnivore	Present study
Lucicutia grandis	NW Pacific	1000–6000	(2)	carnivore on jellyfish	Chindonova (1959)
Pleuromamma robusta	Volcano 7	1259–1332	(8)	carnivore	Present study
	Antarctic	0–1000	(24)	omnivore	Hopkins (1985)
	Sargasso	1000–2000[a]	(13)	mostly detritivore	Harding (1974)
Scaphocalanus major	Volcano 7	775–880	(2)	detritivore/omnivore	Present study
	Sta Catalina Ba.	1300	(1)	amorphous	Gowing and Wishner (1986)
	Sargasso	1000–2000	(1)	detritivore	Harding (1974)
Scolecithricella sp.	Volcano 7	1259–1332	(12)	detritivore, carnivore, omnivore	Present study
	Sta Catalina Ba.	1250	(1)	carnivore	Gowing and Wishner (1986)
Scolecithricella (4 spp.)	Antarctic	0–1000	(77)	omnivore	Hopkins (1985)
Spinocalanus sp.	Volcano 7	2945–3100	(2)	detritivore/omnivore	Present study
	Sta Catalina Ba.	1250	(1)	detritivore	Gowing and Wishner (1986)
Spinocalanus (3 spp.)	Antarctic	0–1000	(45)	mostly phytophagous, small particle-feeders	Hopkins (1985)
Spinocalanus magnus	Sargasso	1000–2000	(10)	detritivore/omnivore	Harding (1974)
Spinocalanus (6 spp.)	Sargasso	3000–4000	(12)	detritivore	Harding (1974)
Undinella sp.	Sta Catalina Ba.	1300	(17)	detritivore, carnivore	Gowing and Wishner (1986)
Undinella sp. V1	Volcano 7	775–880	(5)	carnivore	Present study
Undinella sp. V2	Volcano 7	1259–1332	(6)	carnivore	Present study
	Volcano 7	2945–3100	(5)	carnivore	Present study
Xanthocalanus spp.	Volcano 7	775–880	(7)	mostly detritivore	Present study
	Volcano 7	1259–1332	(1)	detritivore	Present study
	Volcano 7	2945–3100	(1)	detritivore	Present study
Xanthocalanus sp.	Sta Catalina Ba.	1300	(17)	carnivore, omnivore detritivore	Gowing and Wishner (1986)
Boreomysis sp.	Volcano 7	731–752	(9)	detritivore, omnivore	Present study
	Antarctic	0–1000	(2)	omnivore	Hopkins (1985)
Boreomysis (several spp.)	Pacific	Abyssal	(53)	herbivore, carnivore	Chindonova (1959)

[a] Possible contaminant from shallower water

contents of the entire gut and whole cells and organisms. Sample preparation is faster than for TEM, and larger sample sizes can thus be examined. TEM allows detailed examination of a relatively small sample of the gut contents. Identification of nano- and microplanktonic cells is possible, and one can sometimes identify particles embedded in partly digested tissue. Contents do not need to be spread into a monolayer for TEM examination, so detrital particles inside soft-bodied prey can be discerned. Some "amorphous" material can be identified with TEM, but as Gowing and Wishner discussed, some gut contents remain amorphous even with the resolution of TEM. The trophic categories for the same species or genera from different studies agree fairly well. The differences could represent geographic variability, variability in feeding within a species or group, or biases in methods of analysis. Considerable overlap between the categories of detritivore and omnivore would be expected if many of these organisms feed on larger particles that have sunk from surface waters. These particles are microcosms (reviewed by Alldredge and Silver 1988), and ingestion of such a particle could include ingestion of associated small metazoans.

Particles and organisms ingested

The similarity of particulate food consumed by particle-feeding copepods and phaeodarian radiolarians at the three sites appears to reflect the similarity of particles and organisms available for consumption at these sites; we could detect no particles or organisms unique to a site. The two copepod genera that were common at the flank and base (the carnivorous *Undinella* sp. and the detritivo-

rous *Xanthocalanus* spp.) had similar gut contents at both sites. Furthermore, there was no consistent pattern among the types of particles sampled at the sites. Abundances and biomasses of some of the suspended protozooplankton were lowest at the base, but many of the differences were not statistically significant. At the flank and the base, the percentage of total suspended organic carbon made up of protozooplankton was half the value at the summit, but values at all sites were $<0.1\%$. Differences in "fluxes" of sinking plus resuspended organisms also showed no consistent pattern related to sites, and biomass "fluxes" were similar among sites. In contrast to carbon content of suspended protozoans, the percentage of the total carbon "flux" made up by small protozoans, although only a few percent, was slightly higher at the base than at the upper two sites. There was no convincing evidence that the base was significantly higher in skeletal or fecal particles that would make encountering higher-quality particles less likely by a particle-feeder. Although suspended minipellets were most abundant at the base, "fluxes" of most skeletal particles as well as "fluxes" of minipellets were highest at the summit. C:N ratios of the suspended material were variable, probably because of the small sample sizes and low nitrogen values relative to the blanks. Ratios ranged from 3 to 23 ($N=4$) at the summit, 19 ($N=1$) at the flank, and from 6 to 17 ($N=2$) at the base. C:N ratios of the "flux" material ranged from 7 to 12 ($N=2$) at the base, from 10 to 13 ($N=2$) at the flank, and from 11 to 13 ($N=2$) at the summit. Thus, a chemical measure of particle quality also failed to reveal a distinct pattern among sites.

Sediment properties could influence the feeding of zooplankton through resuspension of food items, through stimulation of heterotrophic production in the water (e.g. in a manner analogous to that reported by Wainright 1987), or indirectly by causing higher abundances of near-bottom microzooplankton that feed on the sea floor. Levin et al. (1991) found no difference in C:N ratios among the three sites. However, the percentage of organic carbon in the sediments was highest at the upper summit (3.4%) and lowest at the flank (0.6%), with the lower summit and base intermediate. Chlorophyll *a* and phaeopigments were higher at the upper and lower summit than at the two deeper sites, and bacteria in the upper 1 cm were lowest in abundance at the flank site. Thus, the contribution of particles and organisms from the sediments probably resulted from a complex interaction of gradients with depth and resuspension by currents.

While it would be difficult to partition resuspended carbon from sinking carbon collected by traps within the benthic boundary layer, we can make a rough estimate using trap data from similar depths from the VERTEX project in the northeast Pacific (Martin et al. 1987). Two of the VERTEX sites were in the eastern tropical Pacific away from seamounts. Traps at 700 m from the two sites collected an average of 9 mg C m^{-2} d^{-1}; traps at 1400 and 1450 m collected an average of 5 mg C m^{-2} d^{-1}, and traps at 1950 and 2000 m (the deepest depths available) collected an average of 5 mg C m^{-2} d^{-1} (G.A. Knauer personal communication). If these values are subtracted from our total organic carbon "fluxes" (Table 5), we can estimate that 19, 21, and 20 mg C m^{-2} d^{-1} were resuspended at the summit, flank, and base, respectively. Thus, resuspended carbon appears nearly equal at the three sites.

In conclusion, the pronounced oxygen-minimum zone intersecting the summit of Volcano 7 appears to markedly affect the feeding ecology of benthic boundary-layer zooplankton at three depths on the seamount. Suspended, resuspended, and sinking particles were similar at the three sites, and the gut and vacuole contents of crustaceans and phaeodarians reflected this. Rapidly sinking organic aggregates and associated cells from surface waters coupled with relatively unaltered transit through the broad oxygen-minimum zone could result in similar types of particles reaching the three sites. The presence of algal cells in guts and vacuoles indicates that both groups of zooplankton are using these sinking particles as food. The large numbers of bacteria-like bodies in several of the zooplankton guts may have resulted from the organisms feeding on a bacterial mat or aggregate whose source was related to the oxygen minimum. The presence of these bodies in 43 to 100% of the particle-feeding zooplankton at the three sites suggests that the bacteria-like bodies are an important food source. As discussed for benthic zonation (Wishner et al. 1990), these findings may have relevance for areas where oxygen minima intersect the sea floor on continental slopes (e.g. the Arabian Sea).

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