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Benthic foraminiferal population fluctuations related to anoxia: Santa Barbara Basin

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Abstract. The pore-water geochemistry and benthic foraminiferal assemblages of sediments from two slope sites and within the central portion of the Santa Barbara Basin were characterized between February 1988 and July 1989. The highest foraminiferal numerical densities (1197 cm^{-3} as determined by an ATP assay) occurred at a slope site in June 1988 (550 m) in partially laminated sediments. In continuously laminated sediments from the central basin, foraminifera were found living (as determined by ATP assay) in October 1988 to depths of 4 cm, and specimens prepared for transmission electron microscopy were found with intact organelles to 3 cm, indicating their inhabitation of anoxic pore waters. Ultrastructural data from *Nonionella stella* is consistent with the hypothesis that this species can survive by anaerobic respiration. However, the benthic foraminifera appear unable to survive prolonged anoxia. The benthic foraminiferal population was completely dead in July 1989 when bottom water O_2 was undetectable.

Introduction

High foraminiferal abundances have been noted in numerous regions affected by coastal upwelling or dysaerobic (ca. 40 μM O_2 kg^{-1}; sensu Thompson et al. 1985) to completely anoxic bottom water conditions (Phleger & Soutar 1973; see Gooday 1986, Table 7, p. 1361). While these high numerical densities have commonly been reported, it has not been determined why foraminifera are successful under such environmental conditions. Further, it has not been unequivocally demonstrated that foraminifera survive during extended periods of total oxygen depletion, or what effects hydrogen sulfide has upon them.

This study investigates foraminiferal distributions in Santa Barbara Basin, a silled basin that undergoes cyclic bottom water O_2 depletion and replenishment. An adenosine triphosphate (ATP) assay and the conventional rose Bengal staining technique were both used to determine if

specimens were living at the time of sampling. In addition, foraminiferal ultrastructure was examined for intact organelles indicative of a living organism. The ATP method was also used to estimate foraminiferal biomass. Our findings indicate that the benthic foraminiferal population of Santa Barbara Basin fluctuates over time in response to changes in bottom- and pore-water conditions. At least one species has adapted to survive anoxia over short periods.

Study locality

Santa Barbara Basin is a shallow, nearshore basin within the California continental borderland with a sill depth of approximately 475 m and a maximum depth of 627 m (Fig. 1). Water enters the basin from the oxygen minimum zone (OMZ), and circulation within the basin is restricted, resulting in dysaerobic to anoxic bottom waters. In the center of the basin, the diatomaceous sediments are varved, and varve formation has classically been linked to seasonal changes in terrigenous and diatomaceous sedimentation (Hülsemann & Emery 1961). However, the cyclic replenishment and depletion of bottom water O_2 may be a more important controlling factor (Reimers et al. 1990).

Hydrocast data collected by the California Cooperative Fisheries Investigations Program (CalCOFI) indicate that the dissolved O_2 concentrations in the water column of Santa Barbara Basin varied considerably between January 1988 and July 1989, the sampling period of this study (Fig. 2, Scripps Institution of Oceanography, 1988; 1989; 1990). In January and May 1988, O_2 had been replenished in the basin's bottom waters by recent spillover events (Sholkovitz & Gieskes 1971; Reimers et al. 1990). By August 1988, O_2 conditions in the water column deeper than $\sim$490 m were severely dysaerobic ($< 5\ \mu M\ kg^{-1}$). Oxygen was further depleted by October 1988 with observed values of 0.4 $\mu M\ kg^{-1}$ deeper than 555 m, although the analytical uncertainty of Winkler titrations on samples with $< 5\ \mu M\ O_2\ kg^{-1}$ is large. In January 1989, a slight increase in O_2 concentrations was again observed, but O_2 conditions remained severely depleted deeper than $\sim$460 m. During April 1989, a complete profile was not collected, but it appears that spring bottom-water renewal was not extensive between January and April, since both month's profiles overlap between $\sim$510 and 525 m. By July 1989, O_2 was undetectable at 572 m depth. In brief, it appears that only a weak renewal of basin waters occurred between October 1988 and July 1989, so that severely dysaerobic conditions persisted in 1989.

One feature of the sediment/water interface in the center of the basin

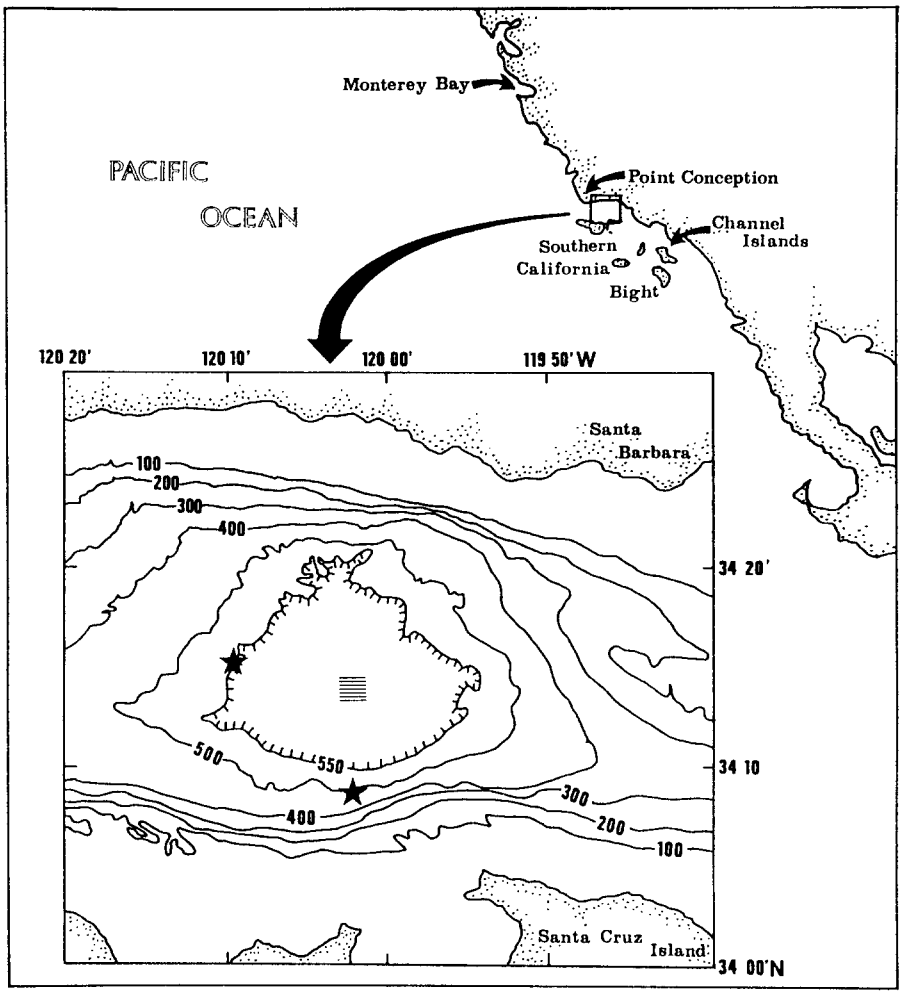

Fig. 1. Map of Santa Barbara Basin and collection sites. Shaded box in the center of the basin shows area where all central basin cores were collected (water depths of cores = 583—589 m; BC8 collected 23 Feb 88, BC21- 25 Feb 88, BC54- 21 Jun 88, BC61- 22 Jun 88, BC68- 24 Jun 88, BC78- 5 Oct 88, BC104- 2 Jul 89, BC105- 3 Jul 89; all laminated sediments). Stars show locations of slope collections (southern slope core [BC19] water depth = 486 m, collected 25 Feb 88, homogeneous sediments; western slope [BC65] = 550 m, 23 Jun 88, partially laminated sediments). Contours in meters.

that is responsive to redox fluctuations is a bacterial mat. The *Beggiatoa* species within the bacterial mat appear to contribute to the deposition of detritus-poor light bands when bottom water O_2 is depleted and pore-water H_2S is available at the sediment-water interface (Reimers et al. 1990).

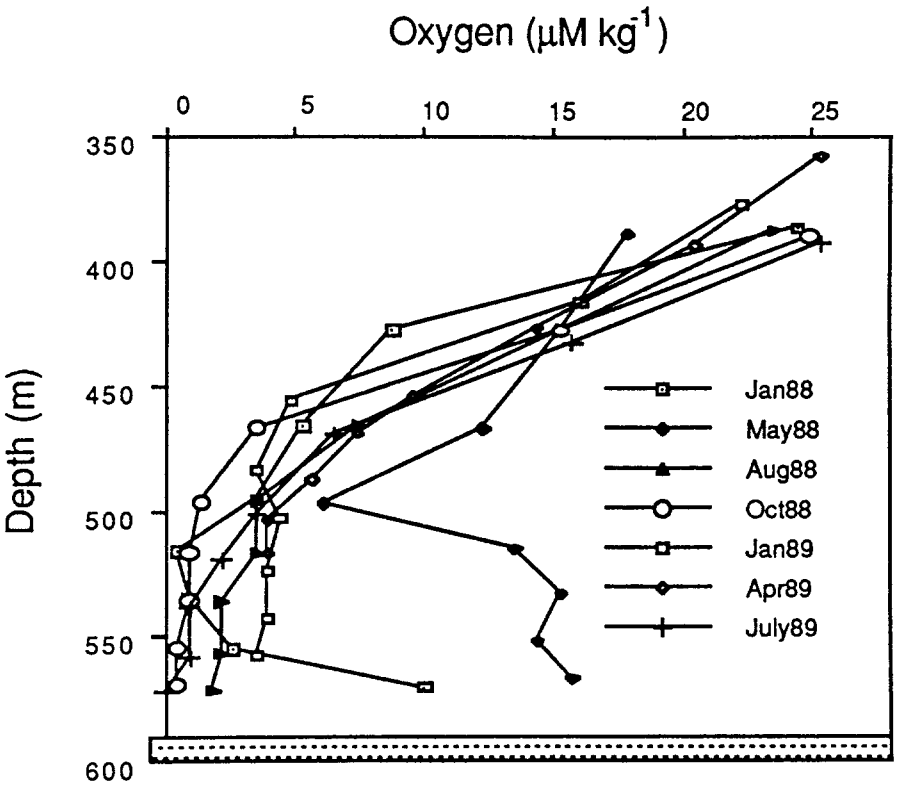

Fig. 2. Water column dissolved O_2 profiles over sampling period. Data collected as part of the CalCOFI program (Scripps Institution of Oceanography 1988; 1989; 1990). Stippled area indicates basin floor.

Surface quarter-centimeter organic carbon values range from 5—8% (dry weight; Reimers et al. 1990) while subsurface values are consistently 3—4% (Schmidt 1990). Surficial sediments situated on the slope of the basin above the sill also have $C_{(org)}$ contents ~ 3—4% (Cary et al. 1989). These slope sediments are homogenized by burrowing infauna (Thompson & Jones 1987). One of the most common macrofaunal species observed on the slope is *Mitrella permodesta*, an epifaunal gastropod, which has also been occasionally observed in boxcores and bottom photographs from the center of the basin.

Methods

Box cores (Soutar-design; 0.1 m^2) were collected four times between February 1988 and July 1989 either near the center, or on the western or

southern slopes, of the Santa Barbara Basin (Fig. 1). Subcores (7.5 cm i.d. butyrate) for pore water analyses were removed from the box cores to a refrigerated van (~ 6 °C; approximate ambient temperature), and sectioned under a N_2 atmosphere into 0.25, 0.5 or 1.0 cm intervals using a device described by Shaw (1989). The period between recovery and complete sectioning was typically less than 3 hours.

Pore-water NH_3 and combined $NO_3^- + NO_2^-$ concentrations were determined using spectrophotometric techniques described by Gieskes & Peretsman (1986). Titration alkalinity was determined on 1 or 2 cm^3 samples using a standard potentiometric titration with O.1N HCl (Gieskes & Peretsman 1986). Sulfate concentrations in pore waters from February (BC19, 21) and October (BC78) cores were analyzed via $BaSO_4$ turbidometry (Tabatabai 1974), however, June samples (BC61) were analyzed using an anion chromatograph (Gieskes & Peretsman 1986). Hydrogen sulfide in samples from BC19 and BC21 was measured using a monobromobimane-HPLC technique (Vetter et al. 1989), while BC68 and BC78 samples were analyzed for ΣH_2S using a mixed-diamine-reagent and spectrophotometry (Cline 1969).

Ammonia and ΣH_2S analyses were initiated within 24 hours of sample collection, and titration alkalinities were determined within one week of collection. Samples, acidified at sea, were analyzed for $NO_3^- + NO_2^-$ after neutralization within 2 weeks of sample collection. Most SO_4^{2-} analyses were done within 2 months of collection; otherwise a Cl^--based correction for evaporation was applied.

Subcores for foraminiferal analyses were sectioned in a manner similar to the pore-water subcores except sectioning was under air. Sediment intervals were sieved using 63 μm screens, the coarser fraction of which were examined under a Wild M5A dissecting microscope at 120 or 250X magnification. Individual foraminifera were mouth-pipetted from sediments, rinsed twice in chilled filtered seawater (0.2 μm), measured for length, and extracted for ATP in hot (95 °C) phosphate/citrate buffer for 5 min (DeLaca 1986; Bernhard 1989, 1990; in press). The number of individuals extracted per interval generally varied between 10—50. Extracts were frozen and later analyzed with an LKB 1250 luminometer for ATP content via a luciferin/luciferase reaction.

As reported by Reimers et al. (1990), total ATP extractions were done on bulk sediments using a cold phosphate buffer (Craven et al. 1986). Extracts were frozen at sea and analyzed using the same luminometer.

A plot of foraminiferal ATP content versus test length yields a significant regression (t-test; $p < 0.001$; Fig. 3A). Examination of these data reveals that no sharp separation between living and dead individuals can be made on this basis. To establish criteria to distinguish living from dead

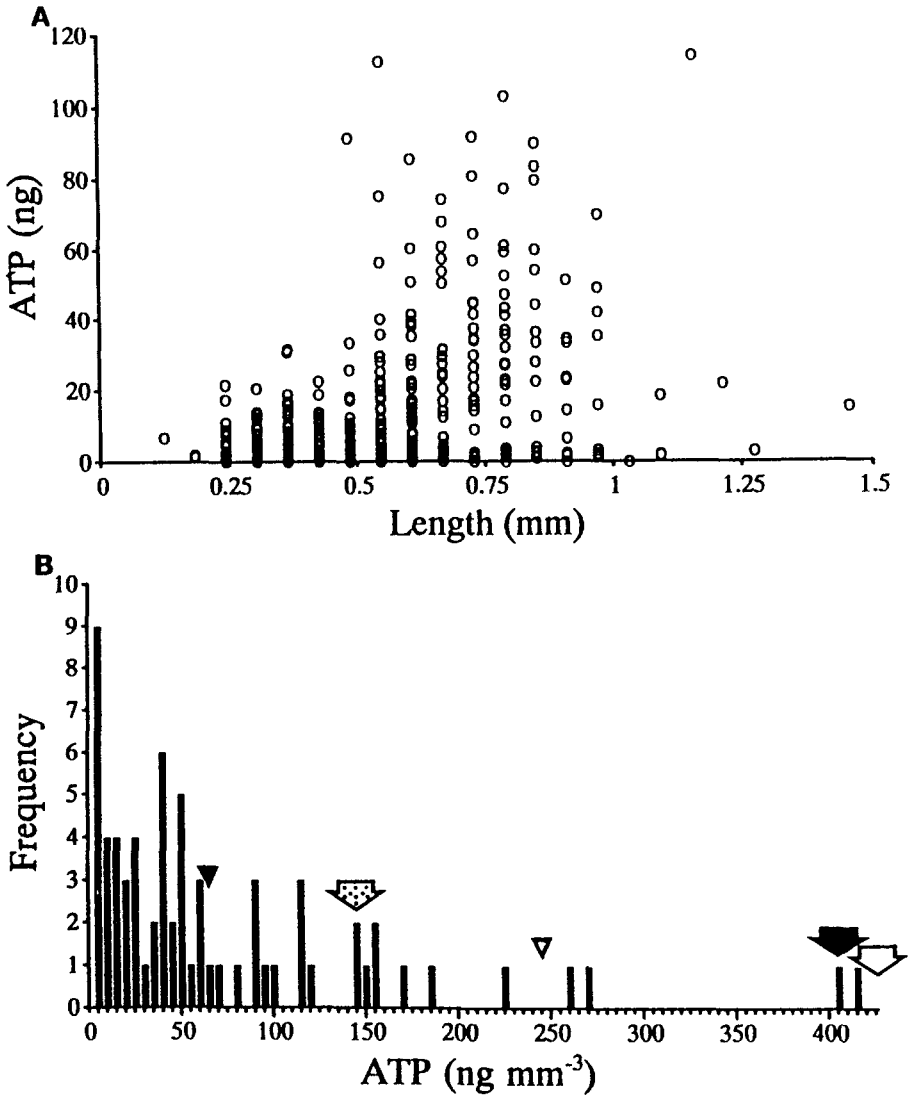

Fig. 3. a. Plot of ATP versus test length for each individual extracted. $n = 761$. b. Frequency histogram of ATP per unit volume for each individual extracted from 4 cm or deeper. $n = 68$. Shaded arrow indicates rose Bengal threshold (see text for details), shaded triangle and open triangle indicate the minimum reported value for algae and bacteria, respectively, by Karl (1980), stipled arrow indicates live/dead boundary for the foraminiferal assemblage off central California (Bernhard in press), and open arrow indicates live/dead boundary for the Santa Barbara Basin foraminiferal assemblage.

individuals, ATP content was expressed on a per unit volume basis. An idealized geometric shape was assigned to each species which was used in conjunction with an individual's measured length and each species' average width to length ratio to estimate individual test volumes. The volume of inorganic material per total test volume was assumed roughly equal between species, since in the Santa Barbara Basin, most common species have equally thin tests.

The criteria to distinguish living from dead specimens in terms of ATP concentration per unit volume was established using a frequency histogram of ATP data from specimens extracted from subcore intervals deeper than 4 cm (Bernhard, in press). The rationale for using these samples is that nearly all individuals at this depth or deeper must be dead because only 0.0047% stained with rose Bengal. The rose Bengal threshold, the lowest possible live-dead boundary, occurs at ~410 ng ATP mm^{-3} on the frequency histogram. One individual possessing 414 ng ATP mm^{-3} was extracted from 8.0—9.0 cm (BC 65), where 99.8% of the individuals were unstained. It is unlikely that such an individual was living at the time of extraction. Further, the only specimens sectioned for electron microscopy from 3—4 cm were obviously dead individuals ($n = 3$). Therefore, the live-dead boundary was taken to be 415 ng ATP mm^{-3}.

Foraminiferal ATP concentrations were used to estimate foraminiferal biomass. The average of the only two precise C:ATP ratios published for foraminifera (C:ATP = 291 and 309; DeLaca 1986), a value of 300, was multiplied by the corrected average ATP content per living individual and by the calculated numerical density of living foraminifera for that interval. The corrected average ATP content per living individual was calculated for each core by subtracting that core's average ATP content per dead individual from that core's average ATP content per living individual. This manipulation helps exclude any bacterial ATP contribution (represented by the 'dead' ATP content) from the foraminiferal biomass estimates. This method to estimate foraminiferal biomass is not dependent upon test volume estimations.

Once a sediment interval had been sampled for specimens intended for ATP extraction, the remainder was preserved in 5% buffered formalin and later stained for ~12 h with rose Bengal in ethanol. At least 300 foraminifera (stained and unstained) were wet-picked from aliquots of each interval to determine the rose Bengal numerical density as well as total numerical density.

Specimens fixed for conventional transmission (TEM) or high-voltage (HVEM) electron microscopy were obtained and treated in the following manner. From a box core (BC68 for June; BC78 for October), a subcore (2.0 cm i.d. in June; 2.7 cm i.d. in October) was collected from which

sediment intervals (0.25 or 1.0 cm) were sliced and fixed in 6% glutaraldehyde/0.1 M sodium cacodylate buffer (pH = 8.1; 6 h; 4 °C). The time from recovery to fixation was ~30 min. After rinsing, sediments were kept in chilled 0.15% sodium azide/buffer until, in the laboratory, individual specimens were osmicated (1% OsO_4/0.1 M buffer; 3 h), decalcified (4% uranyl acetate, aq; 8 h), serially dehydrated in ethanol, cleared in propylene oxide, and embedded in Araldite/Epon 812.

Specimens were cut into 70 or 250 nm sections with a Sorvall MT6000 automated microtome which were stained with 2—3% uranyl acetate followed by Sato's lead/citrate solution. Sections were examined with either a Philips 201 transmission electron microscope or the high-voltage electron microscope of the Wadsworth Center for Laboratories and Research, New York State Department of Health, Albany. HVEM was performed to increase the amount of cytoplasm since evidence of adaptations for anaerobic respiration were sought.

Results

Geochemistry and total ATP

The geochemistry of the interstitial waters varied substantially between collection sites (slope vs. center basin) and, to a lesser extent in the central basin, over time (Fig. 4). Cary et al. (1989) have reported and discussed the geochemistry of BC19, the core from the shallowest site addressed here. This site (486 m) appeared extensively bioturbated and possessed ammonia and titration alkalinity profiles which were nearly constant downcore, in contrast to the increasing concentrations of those constituents downcore at the other locations. The 550-m slope core (BC65) exhibited titration alkalinity and NH_3 profiles intermediate between those of the shallow slope and basin cores. Concentrations of SO_4^{2-} decreased more rapidly with depth in central basin sediments than in slope sediments. $NO_3^- + NO_2^-$ concentrations for center basin cores were, in two cases, unusually high just below the sediment-water interface, but decreased to undetectable levels by 3 cm depth. The same constituents in pore waters from the shallow slope core were always below bottom water concentrations and at detectable levels deeper than 10 cm. Of the cores analyzed for ΣH_2S, only BC78 (basin, October) had detectable sulfide shallower than 3 cm.

Total ATP concentrations increased from February to October, 1988 in the central basin (February data not given, see Reimers et al. 1990). Above 1 cm, October values were 2 to 7 times higher than comparable values for June (Table 1; Reimers et al. 1990).

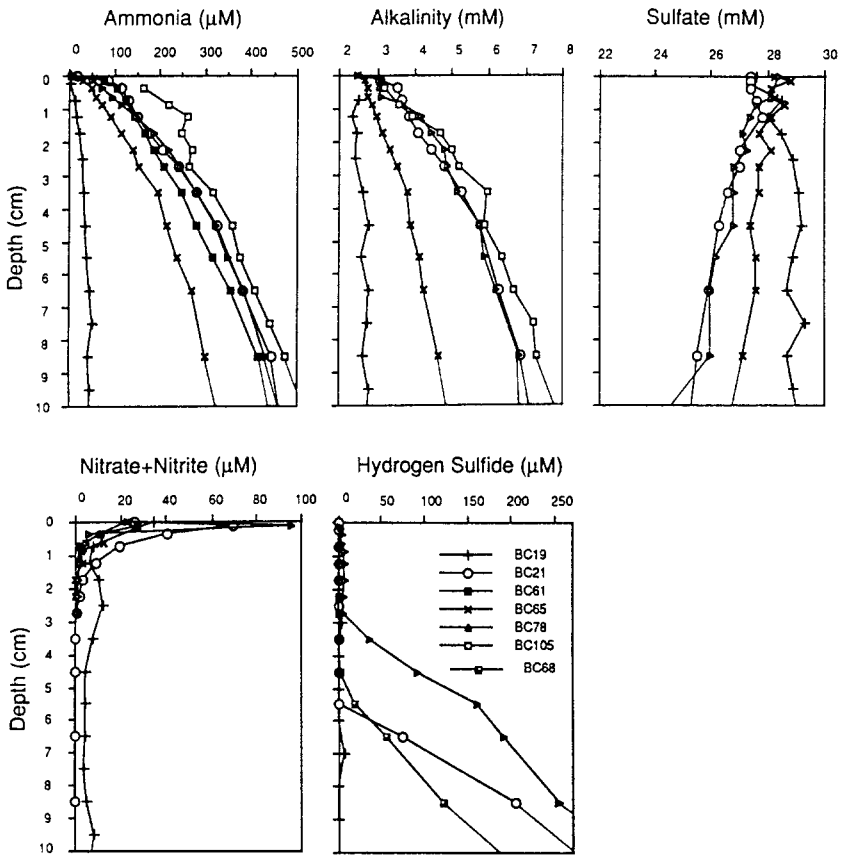

Fig. 4. Profiles of ammonia, total alkalinity, sulfate, nitrate + nitrite, and total dissolved sulfide for all cores analyzed. Each core is depicted by the same symbol throughout the figure. Note that ΣH_2S distributions were not determined in BC61, but are reported for BC68, another June 1988 core which in this study was sampled for electron microscopy.

Foraminiferal abundance, biomass and species composition

The box core collected from the western slope (BC65; 550 m) had the highest abundance of living foraminifera (1197 cm^{-3}; 1978 stained cm^{-3}) and the highest foraminiferal biomass (11.7 mg C cm^{-3}) in the surface sediment interval (0—0.25 cm; Figs 5, 6). The shallower slope station (BC19; 486 m) had much lower numerical densities (53 stained cm^{-3}; 0—1 cm; no ATP data available).

Foraminiferal abundances in sediments collected from the center of the basin varied strikingly between collections (Fig. 5). The surficial sediment numerical density of stained individuals in February, 1988 (BC21) was

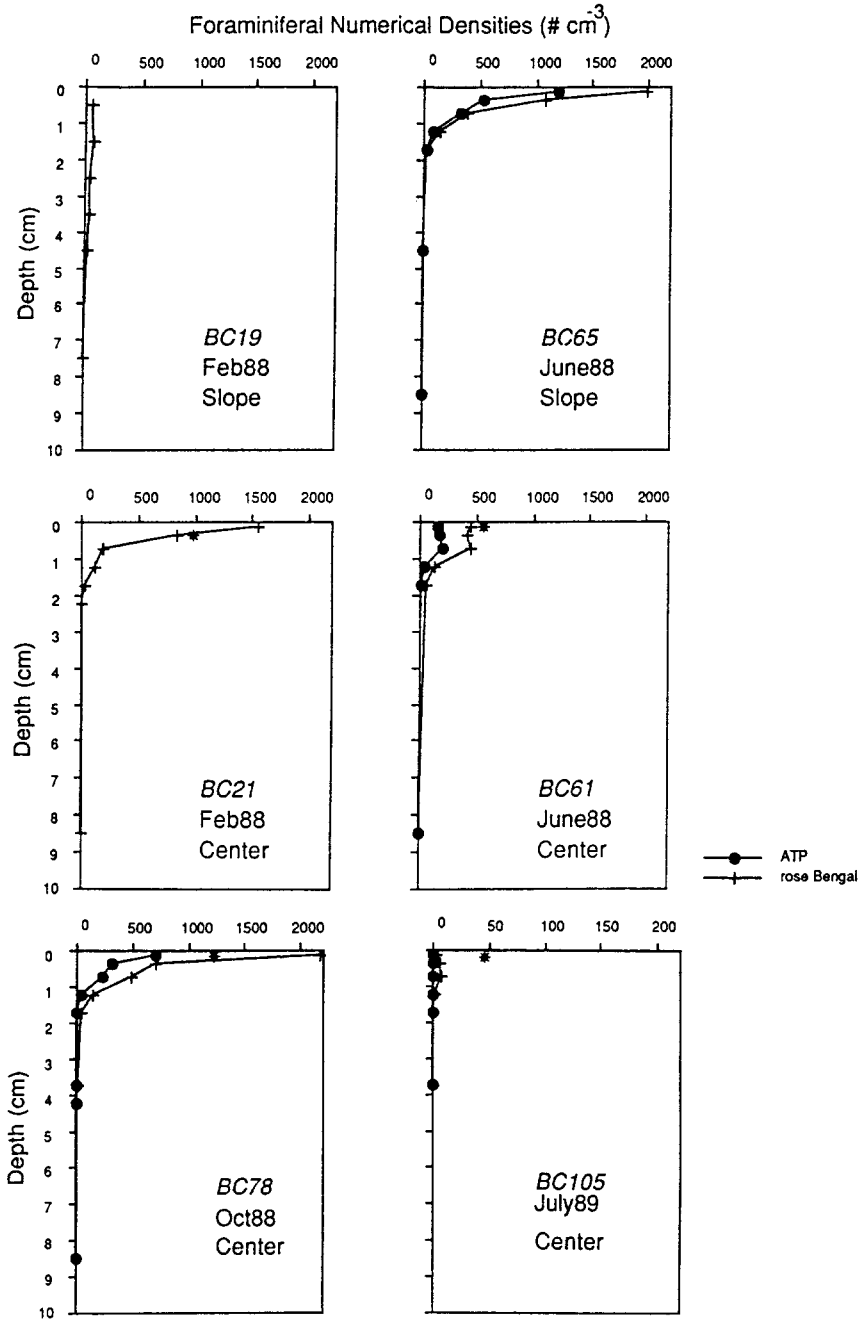

Fig. 5. Foraminiferal numerical density profiles determined by the ATP method or rose Bengal method for all cores. BC19 and BC21 were not analyzed for foraminiferal ATP. Asterisks indicate rose Bengal numerical densities for replicate box core surficial samples (see text; BC8 for Feb 88, BC54 for Jun 88, BC82 for Oct 88, DC104 for Jul 89).

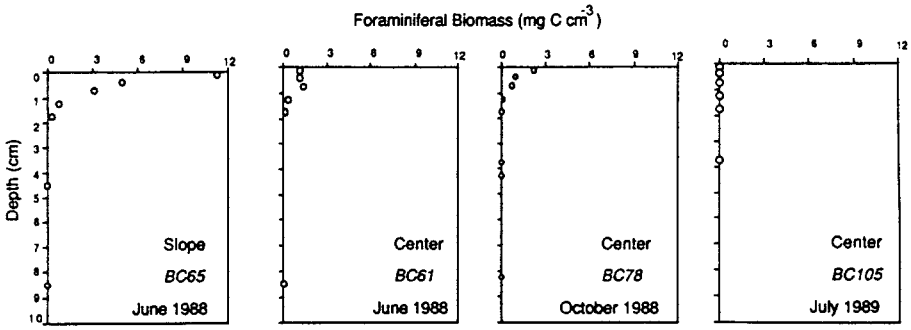

Fig. 6. Foraminiferal biomass profiles for all cores analyzed for foraminiferal ATP.

high (1548 cm^{-3}), moderate in June (BC61; 442 cm^{-3}), very high again in October (BC78; 2176 cm^{-3}), and foraminifera were virtually absent during the last sampling period, in July 1989 (BC105; 3 cm^{-3}). The numerical density of living individuals as determined by ATP showed a similar trend where the density in June (BC61) was 164 cm^{-3} while that of October was over four times higher (706 cm^{-3}). No living specimens were found in July by the ATP method. Estimates of foraminiferal biomass in central basin surficial (0.25 cm) sediments for June were half those for October (1.1 vs. 2.2 mg C cm^{-3}, respectively; Fig. 6). However, biomass estimates were similar (1.3 vs. 1.2 mg C cm^{-3}, respectively) when averaged over the top centimeter.

The shallowest slope core (BC19) had a slight subsurface maximum in abundance of stained individuals between 1—2 cm (no ATP measurements were made on this core). The other slope core (BC65) exhibited a sharp decline in downcore abundances of both living and stained individuals, especially over the top 1.0 cm. Stained individuals were found in the deepest intervals analyzed for both slope cores.

Two of the basin-floor cores (BC21 and 78) exhibited sharp decreases in abundance of living and stained foraminifera with depth. In BC61, the number of living individuals obtained a maximum between 0.5—1.0 cm and stained abundances remained relatively constant over the top 1.0 cm. BC105 had no living individuals and few stained, even at the surface. Stained specimens disappeared from the central basin sediments at shallower depths than was observed in slope cores.

Benthic foraminifera appear to have contributed substantially to total sediment ATP values (Table 1). Data shows that in many intervals benthic foraminiferal ATP estimates were roughly equal to total ATP estimates. In one interval of BC61 (0.5—1.0 cm) the calculated foraminiferal ATP contribution far exceeded that of the bulk sediment. One specimen of *Fursenkoina cornuta* which was extracted from this interval accounted for

Table 1. Total downcore ATP concentrations (ng ATP cm^{-3}; with standard deviation) compared to foraminiferal ATP contribution from the two cores analyzed for both constituents.

Box core	Depth (cm)	Foram ATP	Total ATP $\bar{x}$	Total ATP s
61	0—0.25	3.8	7.4	0.7
	0.25—0.5	3.8	4.4	0.1
	0.5—1.0	4.5	1.1	0.4
	1.0—1.5	1.0	0.4	0
	1.5—2.0	0.4	0.2	0
	8.0—9.0	0	0.1	0
78	0—0.25	7.4	17.7	1.8
	0.25—0.5	3.3	30.8	0.9
	0.5—1.0	2.4	4.3	3.2
	1.0—1.5	0.5	0.7	0.4
	1.5—2.0	0	0.5	NA
	3.5—4.0	0.1	0.1	0
	4.0—4.5	0	0.1	0
	8.0—8.5	0	0.1	0

81 ng ATP. Computing foraminiferal ATP without this specimen resulted in an estimate of 3.7 mg cm^{-3}, still ~2.7 times higher than the highest replicate of total ATP estimates. The foraminiferal ATP contribution in October was similar in magnitude to that of June but proportionally less compared to total values.

Benthic foraminiferal species richness for the top centimeter in the basin was comparable to that of the slope (15—17 versus 14—17, excluding BC105 where species richness = 6). Shannon diversity indices for the surface samples were similar with slightly higher equability in the basin (H'_{basin} = 0.64—0.70; H'_{slope} = 0.63—0.64; BC105 H′ = 0.13). Detailed species occurrence data is presented in Bernhard (1990). Two of the most common species of the basin assemblage, *Chilostomella ovoidea* and *Nonionella stella*, only rarely occurred in slope sediments. *Fursenkoina cornuta* and *Bolivina spissa* were abundant on the slope but were only occasionally found in sediments of the central basin. *Textularia earlandi*, the only abundant agglutinated species, was most abundant in slope core BC65, but was also quite common in the basin. *N. stella* accounted for 83% of the stained specimens in July. Stained *N. stella* also occurred deeper in basin cores more commonly than other species. *C. ovoidea* exhibited a distinct subsurface maximum in BC61, but an abundance pattern which decreased with depth in BC78. The three common basin species (*C. ovoidea, N. stella, T. earlandi*) were all more numerous in October (BC78) than any other sampling period.

Foraminiferal ultrastructure

Specimens collected from nearly 600 m water depth experience a large change in hydrostatic pressure. Most foraminifera examined by TEM appeared to have intact organelle membranes (12 of 19). Electron microscopic investigation of specimens collected in June and October revealed intact mitochondria and smooth endoplasmic reticulum (ER) in many specimens collected from up to 3 cm depth in the sediment column (Fig. 7). One specimen (*Nonionella stella*) was sectioned thoroughly enough to exhibit a well-preserved nucleus (Figs 7A, B).

The youngest chamber of *Nonionella stella* was enveloped by an interlamellar void containing bacteria (Fig. 7D). These chambers also possessed numerous mitochondria, abundant lipid droplets, and food vacuoles. One very large vacuole was typically present in each *N. stella* chamber. Numerous cisternae of smooth ER were observed in *N. stella*. Associated with these thick stacks were granular ER (Fig. 7B), glycogen rosettes (Fig. 7C), and numerous peroxisomes (Figs 7B, E). The close association between peroxisomes and ER has been noted in a few other foraminiferal species (Nyholm & Nyholm 1975).

Chilostomella ovoidea, which comprised the majority of sectioned living individuals (10 of 12), were observed to possess numerous mitochondria in addition to smooth ER and peroxisomes (Fig. 8A). *C. ovoidea* cytoplasm was densely packed, but very vacuolated; food vacuoles containing what appear to be *Beggiatoa* remains were observed in many vacuoles (Fig. 8B). *C. ovoidea* individuals with smooth ER, peroxisomes and mitochondria were found to depths of 3 cm in October.

Observation with HVEM revealed that some fixed specimens did not possess any recognizable cytoplasm (n = 7). Remains included sedimentary debris, relict stercomata, collapsed cell membrances, and pore plates (Fig. 8C). Two individuals were observed with a portion of 'decaying' cytoplasm (e.g. ruptured vacuoles) while other chambers appeared in good health (e.g. intact mitochondria and smooth ER). These specimens may represent the 'resting phase' as proposed by Linke (1989) in which portions of cytoplasm may be resorbed.

Discussion

Methodology

Historically, distinguishing living from dead foraminifera has been problematic (Walton 1952; Walker et al. 1974). The ATP method used here, despite the previously discussed uncertainties, gives a more reliable and

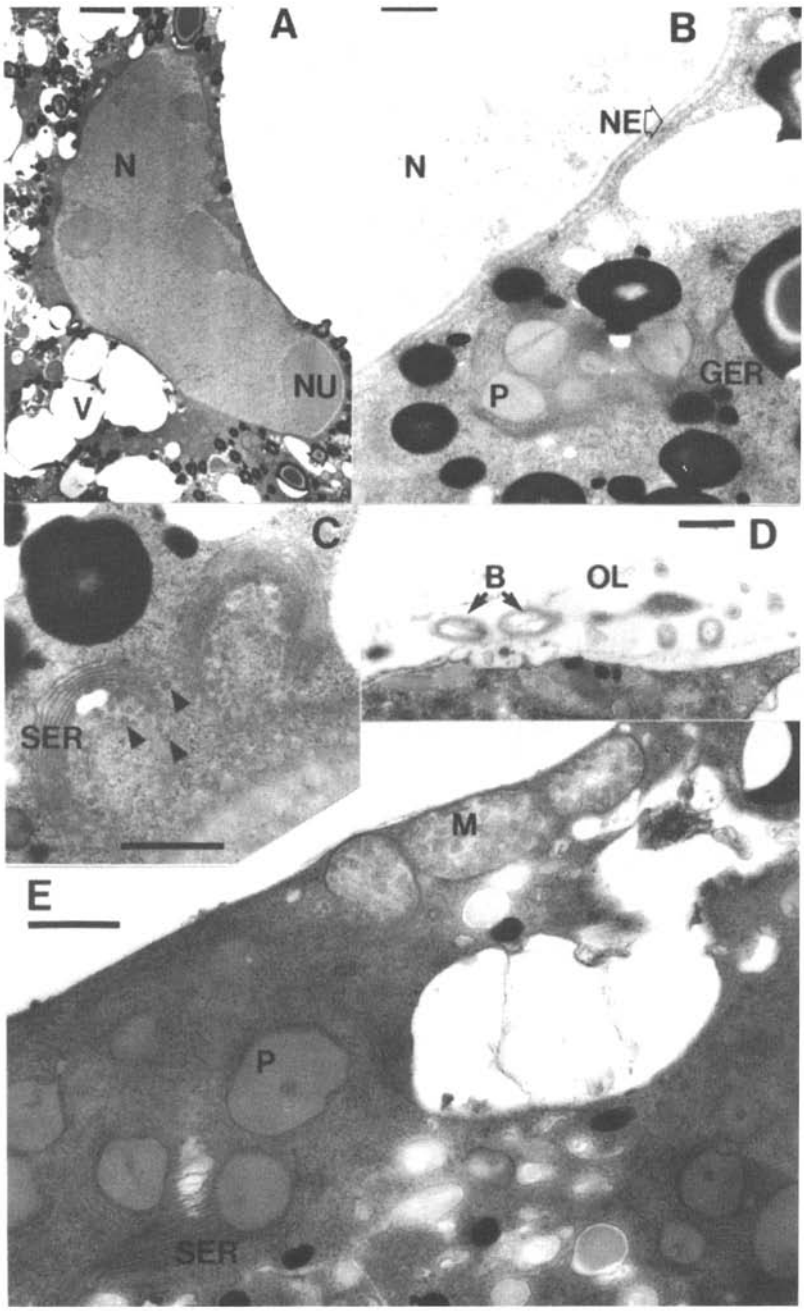

Fig. 7. Photomicrographs (75 nm sections) of *Nonionella stella* collected from BC68, 0—1 cm in October, 1988. a. Overview showing abundant vacuoles (V) in the cytoplasm and the large nucleus (N) possessing numerous nucleoli (NU). Scale bar = 2 μm. b. Nuclear envelope (NE), peroxisomes (P) and granulated endoplasmic reticulum (GER). Scale bar = 0.5 μm. c. Smooth endoplasmic reticulum (SER) and associated glycogen rosettes (triangles point to individual rosettes). Scale bar = 0.5 μm. d. Interlamellar bacteria (B) within the organic lining (OL) of the youngest chamber. Scale bar = 0.5 μm. e. Mitochondria (M), peroxisomes (P) and numerous thick stacks of smooth endoplasmic reticulum (SER). Scale bar = 0.5 μm.

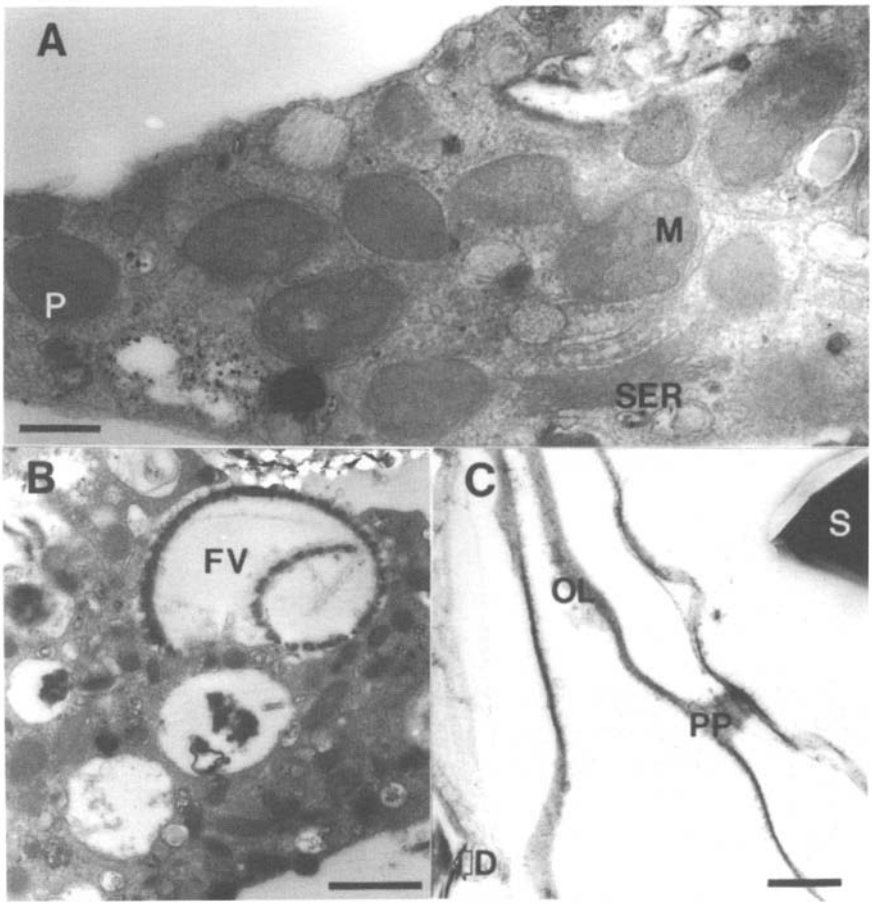

Fig. 8. a and b. Photomicrographs (75 nm sections) of *Chilostomella ovoidea* collected from BC68, 2—3 cm, October, 1988. a. Numerous mitochondria (M) along with peroxisomes (P) and smooth endoplasmic reticulum (SER). Scale bar = 0.5 μm. b. Food vacuole (FV) containing what appears to be *Beggiatoa* remains. Scale bar = 0.5 μm. c. Photomicrograph (250 nm section) of a dead individual with remains of the organic lining (OL) and pore plug (PP). Part of a siliceous particle (S) as well as other debris (D) can be seen. Scale bar = 1.0 μm.

conservative estimate of foraminiferal numerical densities than does the conventional rose Bengal staining technique. Further, the ATP method provides a means for estimating the foraminiferal contribution to total biomass. Ultrastructural data corroborates ATP results. Ultrastructural changes suggestive of degeneration occur quickly after cell death, within hours to days (Elliott et al. 1987; Kerr et al. 1987), although this degradation has not been studied in foraminifera. Thus, the two methods used in this study suggest that numerous foraminifera were alive at collection.

Foraminiferal population attributes

The observed abundances of living foraminifera on the southern slope of Santa Barbara Basin in June (BC65; 1197 cm^{-3}) and in the central basin (BCs61, 78; 164 and 706 cm^{-3}, respectively; excluding July) are very high compared to other abundances investigated using an ATP method (shallow-water Antarctic, ~10—100 cm^{-3}, Bernhard 1989; California slope and rise, 0—31 cm^{-3}, Bernhard in press).

The foraminiferal numerical densities determined in this study are also higher than previously reported using conventional staining for the Santa Barbara Basin and other dysaerobic and anoxic areas. Phleger & Soutar (1973) found central Santa Barbara Basin sediments had numerical densities in the topmost centimeter of ~105—118 stained individuals per cm^{-3} versus 434—693 cm^{-3} (in February, June and October of this study; data averaged over the surface cm). Total foraminiferal abundance (stained and unstained) from one of Phleger & Soutar's two basin sites was comparable to this study's average basin total foraminiferal abundance (753 cm^{-3} vs. 646 cm^{-3}, respectively; data for this study averaged over the surface cm). Comparable stained foraminiferal densities to those observed in this study (2176 cm^{-3}) have been reported only for an area off northern Florida (2181 cm^{-3}, Sen Gupta et al. 1981).

One possible reason for high foraminiferal abundances in the laminated sediments of the central basin is a lack of predators, other than occasional occurrences of the epifaunal gastropod *Mitrella permodesta.* Further, foraminifera are not a major contributor to the diet of this gastropod (Thompson & Jones 1987). Lower foraminiferal densities on the shallow slope are possibly due to more numerous and diverse predators. Another possible reason for high foraminiferal numerical densities in the Santa Barbara Basin is the abundance of food derived from the high $C_{(org)}$ flux and benthic bacterial mat (Hülsemann & Emery 1961; Altenbach & Sarnthein 1989). Also, it has been observed that benthic foraminifera appear to withstand dysaerobic conditions better than any other meio- or macrofaunal group (Josefson & Widbom 1988). A possible explanation for the presence of a thriving foraminiferal assemblage on the basin's lower slope at 550 m, as represented by BC65, is that the geochemical conditions were such that foraminifera were permanent inhabitants while their predators were transients, as evidenced by the occurrence of partially laminated sediments.

The living Santa Barbara Basin foraminiferal assemblage had considerably higher ATP contents per unit volume ($\bar{x}$ = 1180 ng ATP mm^{-3}, s.d. = 1547; n = 172; maximum = 17,358) than those of foraminiferal assemblages from the slope and rise off central California ($\bar{x}$ = 396 ng

ATP mm^{-3}, s.d. = 405; n = 58; maximum = 2,714; Bernhard in press) and from shallow Antarctic waters (Bernhard unpubl.). It is possible that the foraminiferal ATP concentrations were higher in the Santa Barbara Basin because the foraminifera were more actively growing and metabolizing available food. Background ATP concentrations in 'dead' individuals were also higher than in other areas studied indicating either that bacteria were attached to dead tests or that geochemical conditions caused ATP preservation in dead individuals. The latter occurrence has been observed for senescent bacterial cells in anoxic, hypersaline brines of the Gulf of Mexico (Tuovila et al. 1987).

Foraminiferal biomass estimates for this study are about an order of magnitude higher than estimates of foraminiferal biomass obtained using the same methods from off central California (Bernhard in press) and about two orders of magnitude higher than estimates for other areas (Snider et al. 1984; Altenbach & Sarnthein 1989) obtained using various other methods.

Benthic foraminifera contribute substantially to the total ATP (and, therefore, biomass) in the Santa Barbara Basin (approximately 50% in the surface cm). The observation that foraminiferal ATP equaled or exceeded total ATP in some horizons is probably a sampling or methodological artifact. It is certain that *Beggiatoa* and other bacteria were always present in the sediments, and would have contributed substantitally to total ATP concentrations. We conclude that extraction efficiencies were at least partially responsible for the observed results, since a small sample volume (0.5 cm^3), which may not be representative of overall densities, was analyzed for each sediment ATP assessment and a hot buffer was used for foraminiferal extractions while a cold buffer was used for sediment extractions (Karl 1980).

Since replicate cores were not analyzed for ATP, it is not possible to evaluate if foraminifera were patchily distributed on the scale of hundreds of meters throughout the center of the Santa Barbara Basin during this study. However, surface sediments from replicate cores were analyzed using the rose Bengal method (asterisks; Fig. 5). These estimates are similar to those rose Bengal numerical densities of completely analyzed cores, suggesting that the observed foraminiferal population fluctuations are due to a temporal response rather than patchy distributions.

Further support for the conclusion that the observed variations in numbers were temporal variations exists since profiles of total foraminifera were similar when corrected for new sedimentation (Fig. 9). These profiles also indicate that total abundances, when integrated over 10 cm depth in June and July, were much lower than integrated totals in February and October. Dissolution of calcareous species may account for losses of dead

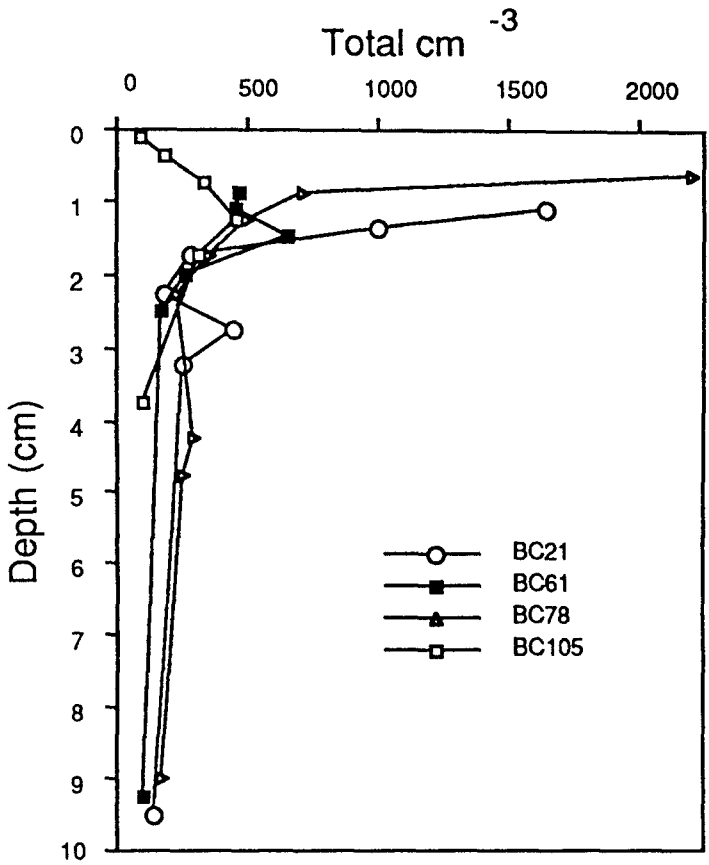

Fig. 9. Total foraminiferal (stained + unstained) numerical densities for all basin cores, adjusted for sedimentation between sampling periods. The adjustment was made by shifting the depth scale using an estimated sedimentation rate of 1.0 cm yr^{-1} (Reimers et al. 1990).

individuals since both June and July exhibited subsurface maximal abundances that are lower in number but correspond in time to surface February and October values. Variation in total foraminiferal densities on a smaller scale could also be caused by vertical migration throughout the top few centimenters of the sediment column as observed for some shallow-water species (Severin & Erskian 1981). For instance, if foraminifera migrated to surficial sediments between June and October, which may be expected with declining O_2 concentrations and shoaling detectable ΣH_2S, the maximum of total numerical densities would be shallower for BC78 than for BC61, as observed.

It is important to realize that the presence of living foraminifera substantially below the sediment/water interface in laminated sediments cannot be attributed to transport via bioturbation or the inhabitation of oxygenated haloes associated with burrows or tubes (Meyers et al. 1988).

Although no samples were collected between October 1988 and July 1989, some speculations can be made regarding what may have caused the foraminiferal population to die off. While a flushing of the basin's bottom water appears to occur commonly in the winter-spring, its extent during early 1989 is uncertain. Bottom water O_2 concentrations were determined to be 0 μM kg^{-1} on July 29, 1989 (Scripps Institution of Oceanography 1990). Thus, it can be assumed that the spillover events were at least not as vigorous as usual or that benthic oxic respiration prior to July was enough to totally deplete the bottom water O_2. It is probable that the Santa Barbara Basin foraminiferal assemblage can withstand very low O_2 conditions and even short periods of complete anoxia, as evidenced by ultrastructural studies. However, if no O_2 is available in bottom waters over an extended period (we estimate weeks to months), the foraminifera apparently die.

The time span between foraminiferal death and complete cytoplasmic decay in an environment such as the Santa Barbara Basin is uncertain. However, Corliss & Emerson (1990) have calculated the time to reduce the number of stained individuals in a completely dead population by one-half. This cytoplasmic degradation 'half-life' is 26—730 days for shallow-infaunal deep-sea foraminiferal species. Therefore, the presence of few stained individuals in July indicates that the foraminifera had been dead for a considerable period.

Even though it appears that the foraminiferal population was completely dead in July, it appears that *Nonionella stella* may be able to survive longer than other species, considering that it comprised over three quarters of the stained individuals at that time. Typically ~10% of the total population consisted of *N. stella*. It is unclear how this species can survive extremely low O_2 concentrations, or possibly anoxia. This species may be capable of extending pseudopodial arrays above the sediment/water interface where dissolved O_2 usually occurs, although it seems unlikely that this alone would cause a significant survival differential since other species presumably could do the same. Pseudopodia are known to extend up to approximately ten body lengths in some foraminifera (Travis & Bowser 1991). Therefore, typical *N. stella* individuals could extend pseudopods ~3.5 mm. It is unlikely that individuals living deeper than 5 mm in the laminated sediments of Santa Barbara Basin could extend

pseudopodial arrays into aerated sediments. A possible reason why *N. stella* may be able to survive severe dysaerobia longer than other species pertains to the ratio of surface area to volume and its influence on cell transport. Since *N. stella* are considerably smaller in volume than most other common basin species, they may be better able to deal with lower O_2 tensions via diffusion into the cytoplasm. Alternatively, it is possible that *N. stella* possess the ability to reduce NO_3^- as observed in some protozoans (Finlay et al. 1983).

The ultrastructure of *Nonionella stella* is a clue for explaining its apparent tolerance of extreme geochemical conditions. The bacteria associated with *N. stella* have an undefined role although they may have some function in a symbiotic relationship (e.g. H_2S oxidation). The only symbiotic relationship described in foraminifera is an endosymbiotic algal symbiosis (e.g. Lee & Zucker 1969) although bacteria have been observed within foraminiferal cytoplasm of questionable condition (Heeger 1990). Further, it is unusual that the bacteria are not distributed throughout the cytoplasm as is typical for most protozoan endosymbiotic associations.

Glycogen is the primary storage substrate used in anaerobic metabolism (Hochachka & Somero 1984). Glycogen is often associated with smooth ER and peroxisomes, and it is thought that these organelles are involved in glycogen synthesis (Nyholm & Nyholm 1975; Threadgold 1976). Once anoxic conditions prevail, glycogen stores could be used by *Nonionella stella* until dissolved O_2 returns. In other words, it is possible that *N. stella* utilizes both mitochondrial respiration as well as glycolysis (Nyholm & Nyholm 1975).

While peroxisomes and smooth ER were observed in *Chilostomella ovoidea*, they were less abundant, and ER stacks consisted of only a few cisternae. The ultrastructural evidence suggests that *C. ovoidea* does not produce glycogen stores as extensive as those of *Nonionella stella*, indicating that *C. ovoidea* can not withstand anoxia as long as *N. stella*. However, *C. ovoidea* appeared to have higher densities of mitochondria than *N. stella*. The presence of abundant mitochondria in ciliates capable of nitrate respiration, have been suggested to compensate for the decreased efficiency of nitrate respiration compared to aerobic respiration (Finlay et al. 1981). Thus, while no direct evidence of NO_3^- respiration in *C. ovoidea* has been observed, it is possible that this is the impetus for its numerous mitochondria.

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