

Environmental control of living symbiotic and asymbiotic foraminifera of the California Current

J. D. Ortiz, A. C. Mix, and R. W. Collier

College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis

Abstract. Plankton tows from the northern California Current constrain biological and physical influences on living planktonic foraminifera. In this region, the dominant factors controlling the size and distribution of symbiotic and asymbiotic species are light and food. Food decreases offshore. Light, needed for symbiont photosynthesis, increases offshore as water turbidity lessens. Asymbiotic foraminifera (e.g., right-coiling *Neogloboquadrina pachyderma*, *Globigerina quinqueloba*, and *Globigerina bulloides*), which survive by grazing, dominate the coastal fauna. The most abundant of these species, right-coiling *Neogloboquadrina pachyderma*, did not change in size in response to increasing food. Species that benefit from symbiont photosynthesis (*Orbulina universa*, *Neogloboquadrina dutertrei*, *Globigerinoides ruber*, and *Globigerinita glutinata*) dominate the offshore fauna. Individuals of these species are rare and have smaller shells in turbid waters where light is limited. *G. ruber*, which is near its thermal tolerance limit of $\approx 14^{\circ}\text{C}$, is the only species to demonstrate a clear temperature response. Although temperature may control a foraminiferal species' distribution near the limits of its thermal tolerance, food and light appear to provide the primary control under more favorable thermal conditions. We infer that gradients in food and light can result in quantifiable sedimentary patterns related to oceanic productivity through changes in plankton biomass and turbidity.

Introduction

Approaches used to calibrate the relationship between environmental conditions and planktonic foraminiferal distributions include sediment, laboratory, and field studies. This field study assesses the relationships between living planktonic foraminifera and environmental conditions in the California Current. Specifically, we investigate the relationships among (1) total foraminiferal standing stock and plankton biomass, (2) species standing stock and hydrographic variability; and (3) shell size and environment.

Sediment calibration studies compare modern environmental data to core top measurements of foraminiferal percent abundance, size, and/or isotopic composition. These studies include statistical estimates of a species' "optimum environment" [Hecht and Savin, 1972; Hecht, 1976; Molfino, 1992] and statistical relationships between the environment and planktonic foraminiferal faunas [Imbrie and Kipp, 1971; Loubere, 1981; Molfino et al., 1982; Ravelo et al., 1990; Dowsett, 1991]. Transfer functions derived in this manner usually assume sea surface temperature (SST) is an ecological variable significant to foraminiferal assemblages or is linearly related to some unspecified variable of ecological significance. However, it is difficult to determine a species' growth environment (depth and season) from its sediment distribution (see Welling et al. [1992] for a radiolarian example). It is thus difficult to determine objectively the environmental field(s)

that control the distribution of living foraminifera. Dissolution also removes information from the sediments and obscures the primary relationship between a species and its environment.

Laboratory studies culture individual foraminifera under controlled environmental conditions. Their goal is to determine effects of individual variables on the growth and reproductive potential of planktonic foraminifera [e.g., Bé et al., 1981; Caron et al., 1987; Bijma et al., 1990b]. However, it can be difficult to apply results from these studies outside the laboratory where suites of variables may produce synergistic effects and conditions encountered by the organism change on a variety of timescales. For this reason, it remains necessary to augment laboratory studies with carefully conducted field programs [e.g., Bé et al., 1977]. Sampling tools used in field studies include sediment traps, plankton tow, and pumps. Sediment traps measure integrated faunal flux, the link between living populations, and the fossil foraminiferal record. Tow and pump studies relate foraminiferal standing stock to environmental parameters.

Using 200- μm mesh nets, systematic plankton tow surveys of the Atlantic and Indian Oceans were conducted from the 1950s to the 1970s [e.g., Bé, 1959b; Bé and Tolderlund, 1971]. A primary goal of these studies was to determine the role of temperature on foraminiferal species distribution. These tows lack good vertical resolution (generally 0- to 200-m integrated samples) but demonstrate that (1) most species of planktonic foraminifera live within the euphotic zone [Bé, 1960] and (2) the dominant species can be separated into zoogeographic assemblages [Bé and Hamlin, 1967]. Similar data from the Pacific and Indian oceans were obtained using nets with meshes ranging from 119 to 505 μm in size [Bradshaw, 1959; Smith, 1963, 1964; Berger, 1969, 1971;

Copyright 1995 by the American Geophysical Union.

Paper number 95PA02088.
0883-8305/95/95PA-02088\$10.00

Miles, 1973]. Although intercomparisons of the Atlantic, Indian, and Pacific data sets are complicated by mesh size variation, the large-scale geographic patterns in each data set appear similar [Bradshaw, 1959].

Plankton tow studies using complex samplers like the Multiple Opening Closing Net Environmental Sensing System (MOCNESS) provide concurrent hydrographic measurements and enhanced vertical resolution. These improvements are critical to assessing growth habitats in the field [Wiebe *et al.*, 1976, 1985]. Studies of low-latitude planktonic foraminifera using multiple net plankton tows show that many foraminifera live below the sea surface at the deep chlorophyll maximum (DCM), perhaps in search of food [Fairbanks *et al.*, 1979; Fairbanks and Wiebe, 1980; Bé *et al.*, 1985; Ravelo *et al.*, 1990; Oberhänsli *et al.*, 1992]. Less work has been done on higher latitude faunas using multiple net towing systems. Here we analyze a zonal transect of MOCNESS plankton tows across the California Current to assess the controls on midlatitude foraminifera. Standing stocks from these tows are accompanied by supporting hydrographic data including temperature, salinity, and measures of small and large plankton biomass.

Because phytoplankton and zooplankton provide the bulk of the nutritional requirements for adult heterotrophic planktonic foraminifera [Hemleben *et al.*, 1988], we hypothesize that changes in plankton biomass are mirrored by changes in asymbiotic foraminiferal standing stock. Likewise, it has been suggested that photosymbionts provide much of the nutritional needs of symbiotic planktonic foraminifera [Bé *et al.*, 1981, 1982; Spero and Parker, 1985; Jørgensen *et al.*, 1985]. This implies that light availability should play an important role in the distribution of symbiotic planktonic foraminifera. Determining the spatial and temporal variability of the foraminiferal-plankton relationship provides an important step toward ultimately calibrating the foraminiferal sedimentary record against changes in plankton biomass and biological productivity [Mix, 1989a, b]. To achieve this goal, we address two questions: (1) What are the relative contributions of biological factors (e.g., food and symbiont photosynthesis) and physical factors (e.g., temperature, salinity, and advection) on the distribution of planktonic foraminiferal species and total foraminiferal standing stock? (2) Do midlatitude planktonic foraminifera exhibit the same affinity with the deep chlorophyll maximum as their low-latitude counterparts?

Materials and Methods

Experimental Design and Field Methods

The study sites are part of the "Multitracers" program, a study of the California Current System at approximately 42°N. These locations are excellent test sites due to strong hydrographic gradients over a relatively small geographic region. Field work was conducted during cruises of the R/V *Wecoma* on September 13-27, 1989 (cruise W8909A), and September 17-30, 1990 (cruise W9009A). A cruise of the R/V *Sacajawea* (cruise NH5-19) on July 23, 1991, provided the opportunity to collect a plankton tow sample during an active upwelling event at 44°N. Data from a total of 11 plankton tows using 63- μ m mesh nets are presented (Figure 1). To emphasize the

spatial relationship between the tows, we refer to them by their distance from the coast. Six single-net plankton tows were collected during cruise W8909A using a Puget Sound net. Four MOCNESS plankton tows were collected during cruise W9009A. One single-net tow was collected during NH5-19 using the Puget Sound net. Deep conductivity-temperature-depth (CTD) stations (>1000 m) were sampled across the transect in September 1989 ($n = 14$) and 1990 ($n = 11$), respectively (Table 1). CTD measurements of temperature and salinity were collected during all three cruises. Light transmission was measured only during the W8909A and W9009A cruises. Advanced very high resolution radiometry (AVHRR) sea surface temperature images document the surface thermal structure during cruise W9009A.

The four MOCNESS tows were collected west of the shelf break, which occurs ≈ 95 km offshore. Six or seven MOCNESS samples were collected within the depth interval from 0- to 1000 m at each site. The depth interval for each MOCNESS net was selected while towing by monitoring CTD temperature, salinity, and density observations to sample mixed layer, seasonal thermocline, and subthermocline regions. This paper discusses samples from 0- to 200 m only. Deep-dwelling planktonic foraminifera observed in the samples >200 m are discussed by Ortiz [1995]. The locations of three of the MOCNESS tows correspond roughly with the sites of the Multitracers sediment-trap moorings referred to as "Nearshore" (120 km), "Midway" (280 km), and "Gyre" (650 km) [e.g., Dymond *et al.*, 1992; Lyle *et al.*, 1992; Ortiz and Mix, 1992; Sancetta *et al.*, 1992; Welling *et al.*, 1992]. The Gyre mooring (650 km offshore) is farther west than the location of the 572 km tow; however, hydrographic conditions at the two sites are similar.

The seven Puget Sound net tows were collected with a simple towing system consisting of a conical, 63- μ m mesh net (4:1 net mesh to mouth area) mounted on a 70-cm ring (mouth area 0.385 m²). The W8909A tows were collected along the Multitracers transect at sites 67, 97, 129, 298, 649, and 763 km offshore (Figure 1). These tows were collected over depth intervals ranging from 0-70 m to 0-200 m. The NH5-19 tow (0-20 m) was taken 10 km offshore in 50 m of water. Sample processing for these seven single net tows was identical to the MOCNESS tows, with the exception that standing stock and plankton displacement volume (see below) was not estimated from these samples due to the variable depth intervals. The foraminiferal results from these tows are presented as percent abundance data.

To calculate a comparable percent abundance for the MOCNESS data, we integrated the >125- μ m standing stocks for each species over the 0- to 200-m depth interval and normalized by the total foraminiferal standing stock at each site over the same interval. This depth interval includes all of the living individuals of the species discussed here based on the September 1990 MOCNESS data. Calculations of the September 1990 percent abundance for the intervals 0-70, 0-100, and 0-200 m are essentially the same. Comparison of the single-net tows to the MOCNESS tows is appropriate assuming both sets of tows sampled the water column down to the depth of the deepest species maxima. This depth was approximately 70 m based on the MOCNESS data.

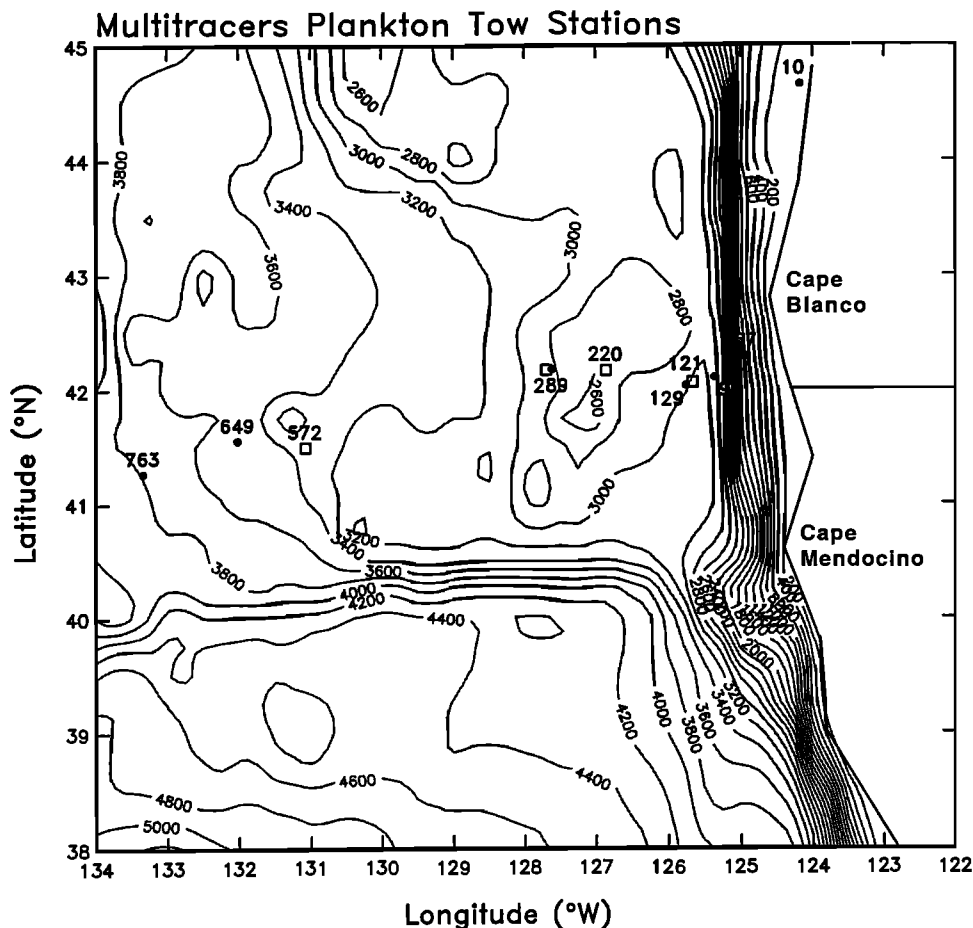


Figure 1. Map of the Multitracers study region. Open squares mark the Multiple Opening Closing Net Environmental Sensing System (MOCNESS) tows, while solid circles mark the single-net tows. Sites are labeled by distance offshore in kilometers. Contours at 200-m intervals are bathymetry at 15-min resolution.

MOCNESS Sample Processing

The MOCNESS samples were preserved at sea in 10% solutions of formalin (buffered to pH \approx 7.5 using NaBO_4) and placed in cold storage for processing on land. The samples were later split to within $\pm 5\%$ by volume using a four-way, OSU sediment-trap splitter [Fischer, 1984]. Quarter splits from each sample were used to determine the number of planktonic foraminifera (125-150 and $>150 \mu\text{m}$) and the wet volume plankton catch ($>63 \mu\text{m}$) collected by each MOCNESS net. The wet volume plankton catch was measured in a graduated cylinder after allowing the plankton to settle.

We distinguished visually between "living" (protoplasm-full) and "dead" (protoplasm-empty) foraminiferal shells. Most samples were analyzed without protoplasm staining. However, Rose Bengal was added to several samples in 1 g/L concentration prior to plankton catch determination and density separation, then allowed to soak for 24 hours [Walton, 1952; Bernhard, 1988]. All foraminiferal data reported here are from protoplasm-full individuals.

Foraminifera were separated from the less dense, nonshelly plankton catch by density separation [Bé, 1959a]. We prefer this method of separating foraminifera from plankton over the

use of hot bleach, peroxide [Sautter and Thunell, 1991], or low-temperature ashing [Oberhänsli *et al.*, 1992]. Methods other than density separation preclude the possibility of counting protoplasm-full shells, may damage the more fragile foraminifera, and can alter shell isotopic composition if partial dissolution occurs [Ganssen, 1981].

Settling in a saturated solution of NaCl (310 g/L, specific gravity 1.20) separates the dense shelly plankters from less dense, nonshelly plankters. The procedure entails pouring aliquots of sample ($\approx 50 \text{ mL}$ at a time) into a clear 1-L beaker of saturated NaCl solution. Small sample aliquots help prevent the foraminifera from becoming entangled in the floating plankton. After the foraminifera settle, the floating material is removed by suction, and the procedure is repeated until the entire sample has been processed. Separation of the planktonic foraminifera from the floating organic matter was not significantly size dependent. Seven randomly selected sample pairs indicate only $19 \pm 14\%$ of the 125- to $150\text{-}\mu\text{m}$ size class and $10 \pm 6\%$ of the $>150\text{-}\mu\text{m}$ size class became entangled. We inspected the residual floating material under magnification and wet-picked any remaining foraminifera. The separated foraminifera were then transferred to glass petri

Table 1. W9009A and W8909A Deep Conductivity-Temperature-Depth (CTD) Stations

CTD Station	Cast Depth, m	Latitude, N	Longitude, W	km Offshore	Local Time, PST
<i>W9009A Stations</i>					
90-05	2652	42.375	126.375	184	00:05
90-06	1502	42.082	126.001	149	22:53
90-07	2952	42.080	126.997	231	04:26
90-08	2751	42.188	127.615	282	09:49
90-14	3400	41.592	131.982	646	13:36
90-17	2502	41.666	131.233	583	07:11
90-18	2951	41.751	130.002	481	13:36
90-19	1500	41.832	128.964	394	21:50
90-20	1500	41.831	128.200	331	03:29
90-23	1002	42.084	125.365	97	22:34
<i>W8909A Stations</i>					
89-04	976	42.160	124.559	67	00:25
89-14	1000	42.006	125.457	129	23:49
89-23	2601	42.086	125.450	129	00:30
89-32	2700	42.091	127.345	279	00:09
89-39	3600	41.331	131.596	648	23:58
89-49	3750	41.151	133.202	763	23:57
89-56	3450	41.349	130.561	560	23:50
89-58	3100	41.420	130.003	482	00:19
89-59	3300	41.549	128.595	396	00:35
89-60	2870	42.049	128.001	314	23:51
89-65	3222	42.202	127.032	238	00:37
89-74	1000	42.072	126.297	190	23:48
89-75	2693	42.059	125.599	149	23:55
89-76	3072	42.047	125.298	107	00:05

dishes, the remaining saline solution was carefully removed by pipette, and the sample was allowed to air dry overnight.

The foraminifera were then dry sieved at 125 and 150 μm . We select these size fractions to facilitate comparison with (1) our 1987-1988 sediment trap study [Ortiz and Mix, 1992], (2) the >125- μm work from the Gulf of Alaska [Sautter and Thunell, 1989], and (3) the >150- μm sediment studies such as Climate: Long-Range Investigation, Prediction, and Mapping (CLIMAP) [1976]. Foraminifera in both size classes were identified to species level using the taxonomy of Parker [1962] and Bé [1977]. The only difference between the taxonomy used here and that used in our 1987-1988 sediment trap study [Ortiz and Mix, 1992] is with the classification of the *Neogloboquadrina pachyderma* - *Neogloboquadrina dutertrei* intergrade category of Kipp [1976]. After careful analysis of the distribution of *Neogloboquadrinid* planktonic foraminifera in the Multitracers sediment trap and plankton tows, we consider the P-D intergrade category to be a morphologic subgroup of *N. dutertrei*. We have grouped these two categories in this paper. This grouping did not affect the results presented here; similar results were obtained when *N. dutertrei* was analyzed without the addition of individuals that some studies have referred to as P-D intergrade.

Foraminiferal Standing Stock (F_{ss}) and Plankton Displacement Volume (P_{dv}) Calculations

Using estimates of the water volume filtered by the MOCNESS, we convert raw planktonic foraminiferal shell counts (N_f) and wet volume plankton catch (V_p) to

foraminiferal standing stock (F_{ss}) and plankton displacement volume (P_{dv}). P_{dv} is a measure of the >63- μm plankton biomass at each site. Because the MOCNESS flow meter failed in September 1990, we estimated volume filtered from tow duration using a linear regression ($n = 45$, $r^2 = 0.97$, $p \leq 0.01$) based on flow meter data from MOCNESS tows [Welling et al., 1991] collected at the same locations in September 1987:

$$V_f = 16.2(t) - 4.7 \quad (1)$$

(in cubic meters). In the above relationship, t is the tow duration in decimal minutes. Residual errors associated with (1) amount to $\leq 12\%$ of the estimated volume filtered. Foraminiferal standing stock (F_{ss}) in shells per cubic meter and plankton displacement volume (P_{dv}) in milliliters per cubic meter were calculated by dividing N_f and V_p , respectively, by the sample split size (S) and volume filtered (V_f). The sample split size (S) was 1/4 in all cases. Counting errors based on the species maximum percent abundance at each site ranged from less <1% to 3% using the method of Dryden [1931]. Splitting, counting, and towing errors produce a total measurement error of 20% for the foraminiferal standing stock estimates (F_{ss}). Total errors in P_{dv} are comparable.

MOCNESS Tow Data Analysis

We present the species' standing stocks as vertical profiles across the transect. Q-mode factor analysis [Klovan and Imbrie, 1971] based on all MOCNESS samples from 0- to 200 m objectively grouped 13 foraminiferal taxa with similar distributions. Prior to the factor analysis a percent-maximum transformation normalized the standing stock of each species in each sample by its maximum standing stock in the entire data set. This preserves the spatial structure of the data set during the factor analysis but ranks all species equally. A varimax rotation optimized the factor solution to give assemblages with mostly positive factor scores.

In the absence of predation and others sources of mortality, a species optimum environment is identified by the location of its maximum growth rate. Our poisoned plankton tow samples preclude the direct measurement of growth rates. Therefore to test the relationship between a species' standing stock and environmental forcing (e.g., light and food requirements, temperature and salinity tolerances, etc.), we assume that (1) the preferred habitat of each species at each site occurs at the depth of its maximum concentration and (2) the magnitude of each species' maximum reflects environmental conditions at that site averaged over the towing interval. In cases where a species is equally abundant within error bars in two samples from the same site (*Globigerinita glutinata* at 220 km and *Globigerina quinqueloba* 121 km offshore), we plot both samples. By focusing on the species' maxima at each site we improve the signal-to-noise ratio and decrease the effects of extraneous factors which might otherwise mask relationships between species distribution and environmental factors. The strength of the observed relationships is assessed using the squared correlation coefficient (r^2) which determines the fraction of variance explained [Snedecor and Cochran, 1989]. Statistical significance is assessed by the associated "p-value" which is reported only for relationships significant at the $\leq 5\%$ or $\leq 1\%$ levels.

Foraminiferal Size Measurements

We supplement the standing stock estimates with shell length measurements to obtain a second, independent measure of foraminiferal success. Shell length was measured using an ocular reticule at 100x magnification ($\pm 6\text{-}\mu\text{m}$ precision). On short timescales, shell size variations should be correlated with a species' growth rate. We selected three abundant species on which to conduct this size analysis, one which harbors obligate endosymbionts (*O. universa*), one which harbors facultative endosymbionts (*N. dutertrei*), and one which does not harbor endosymbionts (right-coiling *N. pachyderma*) [Hemleben et al., 1988]. Our objectives here are (1) to test whether changes in size can be linked to the degree of dependence of the host on its symbionts and (2) to determine if changes in size are correlated with changes in standing stock. The size measurements presented here are from shells collected at the depth of the species' standing stock maxima.

Hydrographic Data Analysis

AVHRR images of September 20, 1990 (22:13:30 GMT), and September 29, 1990 (22:14:40 GMT), from the Scripps Satellite Oceanography Center, were converted to sea surface temperature using the commercially available X-Image software program. The SST values at 42.5°N across the two images were then extracted for intercomparison and cloud masked visually with a simple threshold test [Stewart, 1985].

The CTD used during W8909A and W9009A was equipped with Seabird pressure, temperature, and conductivity sensors. Conductivity was converted to salinity as defined by the 1978 Practical Salinity Scale (PSS-78). Temperature and salinity were used to calculate (1) density as defined by the 1980 International Equation of State (IES-80) and (2) geostrophic velocity relative to an assumed level of no motion at 500 m [Pond and Pickard, 1983].

The CTD was also equipped with the same Sea-Tech transmissometer during both cruises. This instrument measures the attenuation of monochromatic light at 670 nm along a path length of 25 cm [Spinrad, 1986; Spinrad et al., 1989]. This light attenuation is linearly proportional to the particle concentration volume in the water [Zaneveld et al., 1979]. Following standard practice, we present the transmissometer data as C_p , the particle attenuation coefficient. C_p values are influenced most heavily by $<20\text{-}\mu\text{m}$ microplankton biomass [Pak et al., 1988; Gardner et al., 1993]. C_p thus provides a biomass measure weighted toward phytoplankters and small heterotrophs, which complements the P_{dv} estimates of larger ($>63\text{ }\mu\text{m}$) plankton volume.

The attenuation of ambient light in water is proportional to the vertically integrated concentration of particles in the water. To emphasize the spatial pattern of turbidity that attenuates ambient light with depth, we calculate the relative particle load along the transect in September 1989 and 1990. This was done by summing the C_p data from 200 m to the surface at each CTD site and dividing these values by the maximum integrated value obtained in September 1990. This allows for direct comparison of the integrated particle standing stocks from the 2 years by referencing changes to the maximum value in September 1990. Higher surface values imply greater vertically integrated standing stocks of particles and greater light attenuation.

Results

The Physical Environment

The Multitracers transect ranges from cool upwelling-influenced waters near the coast to waters influenced by the oligotrophic subtropical gyre offshore (Figure 2). The prominent cool-water filament situated off Cape Blanco (sampled by the 120 km tow) and its associated anticyclonic eddy to the north are persistent features during the upwelling season [Laur, 1967; Ikeda and Emery, 1984; Strub et al., 1991]. These mesoscale features (Figure 2) carry the influence of coastally upwelled water farther offshore than the ≈ 50 km zone of active upwelling [Huyer, 1983; Strub et al., 1991]. Similar AVHRR SSTs from September 20, and 29, 1990 suggest that the surface thermal structure was essentially unchanged throughout cruise W9009A (Figure 2, inset).

The W9009A and W8909A deep CTD stations provide transects of temperature, salinity, density (σ_t), geostrophic velocity (relative to 500 m), and C_p (Figures 3 and 4). We discuss the September 1990 hydrography first because it accompanies the higher-resolution MOCNESS plankton tows.

During the upwelling season, in response to wind-induced coastal upwelling and intense southward flow, the temperature, salinity, and density isolines outcrop near the coast (Figure 2 and 3). Accordingly, the surface mixed layer is shallowest near the coast and increases in depth to the west. The Columbia River plume, a lens of buoyant, low-salinity water situated 250-450 km from the coast, is evident in the salinity and σ_t transects (Figures 3b and 3c).

The meridional component of geostrophic velocity (relative to 500 m) indicates southward flow throughout most of the transect, with strongest southward flow near the coast and weaker southward transport in the Columbia River plume (Figure 3d). The only significant northward flow occurs between 160 and 220 km offshore in an eddy between the coastal upwelling front and the Columbia River plume. Similar flow patterns are obtained for assumed reference depths of 750, 800, and 1000 m. This northward flow appears to be the extension of the Cape Blanco filament which traverses the 220 km site (Figure 2). Velocities 450-550 km offshore indicate slack water or weak northward transports.

Highest particle attenuation coefficients occur in surface waters near the coast and subsurface waters offshore. Particle attenuation rapidly decreases offshore and with increasing depth (Figure 3e). This pattern indicates turbid, particle-rich water near the coast and less turbid, particle-poor water further offshore. Inshore of 250 km, the particle maximum is largely a surface feature, extending down to 50 m. Offshore of 250 km, the particle maximum becomes a subsurface feature between 20 and 60 m.

The vertically integrated particle load (Figure 3f) closest to the coast (≈ 100 km) is roughly twice as high as that farthest offshore (≈ 600 km). Assuming that the light scattering properties of the particles along the transect are similar, the high particle load near the coast should result in a factor of 2 greater attenuation of light near the coast than farther offshore. Measurements of the diffuse attenuation coefficient (K_d) of ambient photosynthetically active radiation (PAR) at these same sites in September 1991 under similar particle loads demonstrate that the 1% PAR level is achieved at 35 m near the coast (≈ 100 km) and twice as deep at 70 m farther

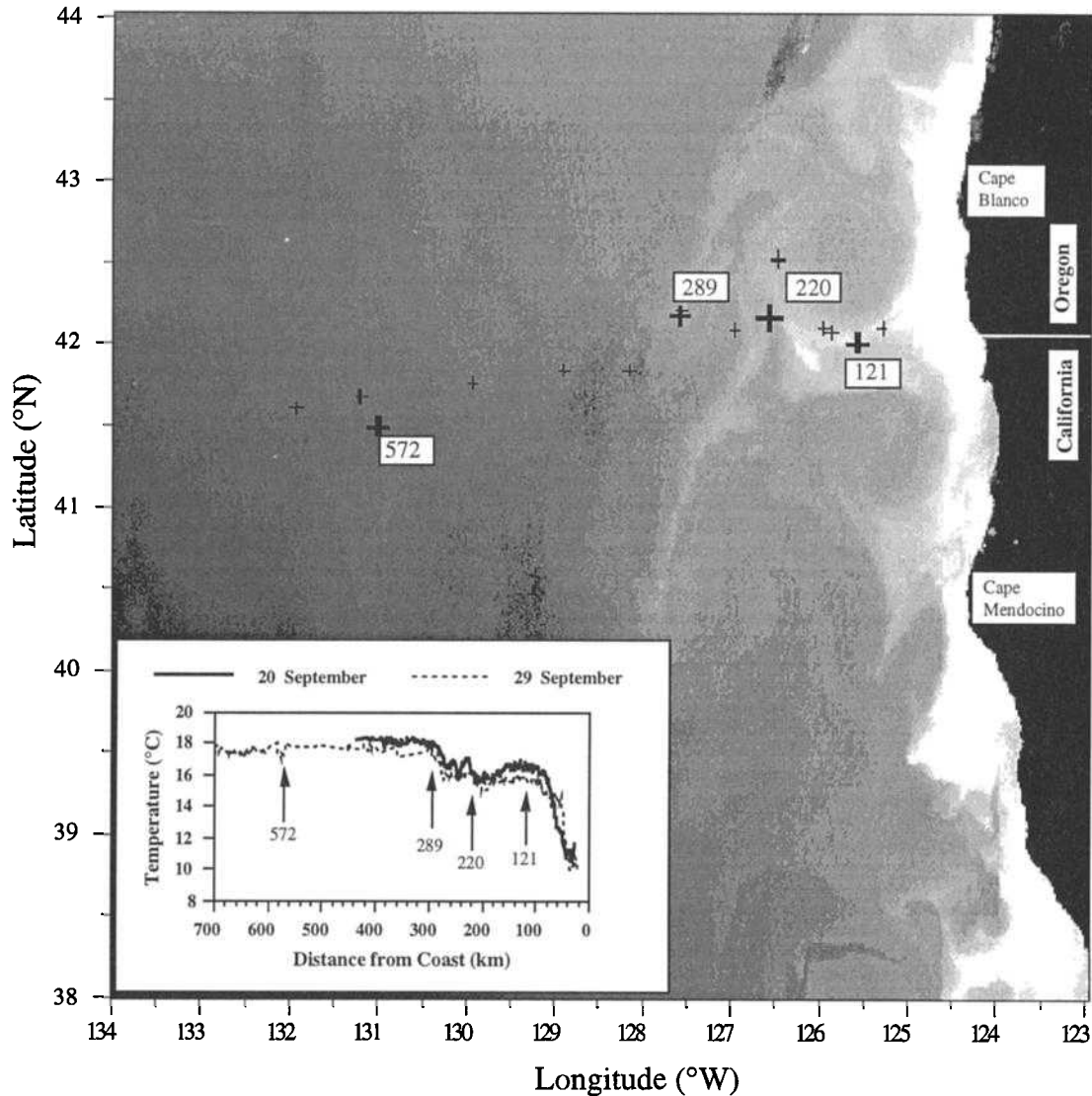


Figure 2. Advanced very high resolution radiometer (AVHRR) image of the Multitracers study area on September 20, 1990 (22:13:30 GMT). Lighter shades near the coast indicate cold upwelled waters ($\approx 10^{\circ}\text{C}$), while heavier shades indicate warmer offshore waters ($\leq 18^{\circ}\text{C}$). Large crosses denote the locations of the four MOCNESS plankton tows: 121, 220, 289 and 572 km offshore. The small crosses denote the locations of the deep conductivity-temperature-depth CTD stations. The insert compares AVHRR temperatures from this image to temperatures from September 29, 1990.

offshore (≈ 600 km) (C. Roesler, Oregon State University, personal communication, 1994).

Hydrographic conditions during September 1989 were qualitatively similar to those of September 1990. Offshore mixed layer temperatures during September 1989 (Figure 4a) were $\approx 2^{\circ}\text{C}$ cooler than during September 1990 (Figure 3a). The Columbia River plume (≈ 32.3 practical salinity units (psu)) was closer to the coast in September 1989 and was much narrower than in September 1990. As a result, offshore waters were saltier in September 1989 (Figure 4b) than in September 1990 (Figure 3b). The changes in temperature and salinity resulted in stronger density gradients near the coast (Figure 4c) and more intense geostrophic flow during September 1989 (Figure 4d). The locations of the high-velocity regions did not change appreciably from their September 1990 locations.

Offshore values of C_p were twice as great during September 1989 (Figure 4e) than September 1990 (Figure 3e). The integrated offshore relative particle load in September 1989 (Figure 4f) was 30-40% higher than in September 1990 (Figure 3f). In September 1989, the 80% particle load contour extends across the entire transect. In September 1990, the 80% contour extends less than 250 km offshore.

Environmental data collected at the time of the NH5-19 tow in July 1991 indicate extremely high biomass and active upwelling [Dickson, 1994]. Temperature over the 0- to 20-m towing interval ranged from 8 to 10°C and salinity ranged from 33.8 to 34.2 psu. These values are colder and saltier than surface conditions along the Multitracers transect and thus provide a reasonable estimate of "end member" seasonal upwelling conditions in the northern California Current.

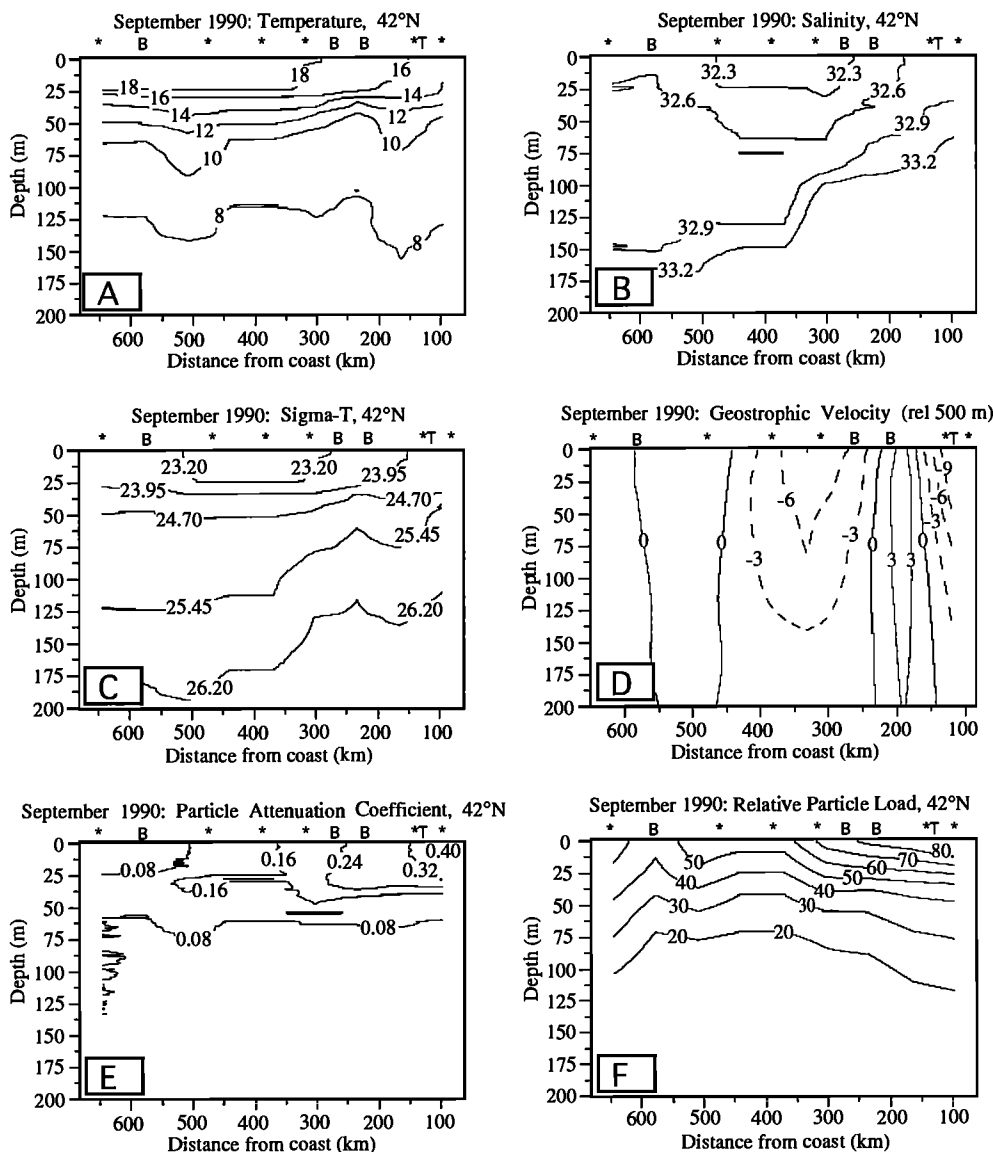


Figure 3. Hydrographic properties (0-200 m) across the Multitracers transect in September 1990, based on nine deep CTD stations located 97-646 km offshore. Symbols across the top of each panel denote CTD locations (asterisks), plankton tow locations (T), or locations where CTD and plankton tows were coincident (B). (a) Temperature data contoured at 2°C; (b) salinity data contoured at 0.3 practical salinity unit (psu) intervals; (c) density (σ_T) contoured at 0.25 kg m⁻³ intervals; (d) meridional component of geostrophic velocity relative to 500 m contoured in 3 cm s⁻¹ intervals; (e) transmissometer particle attenuation coefficient (C_p) contoured in 0.08 m⁻¹ intervals; (f) relative particle load contoured in 20% intervals.

Comparisons of P_{dv} and C_p

In these samples, P_{dv} is dominated by various life stages of small calanoid copepods, euphausiids, and chaetognaths. C_p is predominantly influenced by smaller phytoplankton and microheterotrophs (<20 μ m). For each MOCNESS plankton tow sample, Table 2 lists estimates of the water volume filtered, environmental variables averaged at tow resolution, and total foraminiferal standing stocks. The tow resolution at the Columbia River plume site 289 km offshore is coarser (0- to 60-m) than at the other three sites (0-30 m and 30-70 m). We assess the potential bias associated with this sampling

problem at the averaging the 1-m resolution C_p data into 0- to 60-m and then 0- to 30-m and 30- to 70-m bins. The 0- to 60-m C_p average at the 289-km site (0.186 m⁻¹) is 7% smaller than the 0- to 30-m average (0.200 m⁻¹) and 38% larger than the 30- to 70-m average of 0.054 m⁻¹ (Table 2). Because C_p is highly correlated with P_{dv} and F_{ss} at all sites, we infer that the 0- to 60-m plankton tow at the 289-km site underestimated 0- to 30-m P_{dv} and F_{ss} by 10% at most and overestimated the 30- to 70-m values by 40% at most. The potential bias of +10% from 0- to 30-m and -40% from 30- to 70 m is similar to the measurement error of 20% for P_{dv} and F_{ss} . Such errors would not greatly affect the maximum values of C_p , P_{dv} , and F_{ss} we

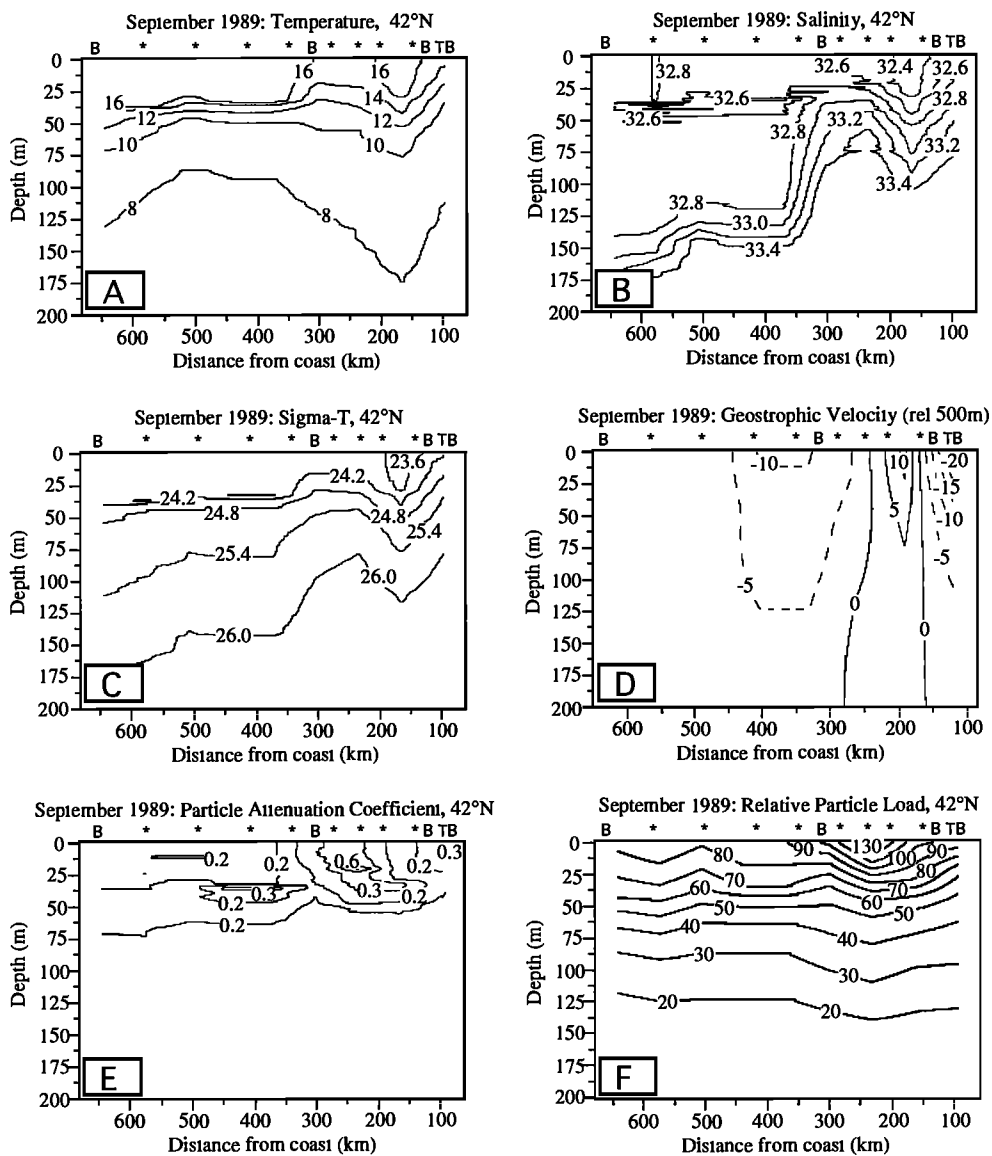


Figure 4. Hydrographic properties (0-200 m) across the Multitracers transect in September 1989, based on 12 deep CTD stations located 107-648 km offshore. Plotting conventions as in Figure 3.

report for the 289-km site. Because our subsequent analyses are based on comparisons of maximal values, we conclude the loss of resolution at the 289-km site is not a serious hindrance.

During cruise W9009A, three of the MOCNESS tows were collected more than 1 hour after sunset at sites 121, 289, and 572 km offshore. The fourth MOCNESS tow, 220 km offshore, was collected 13 min after sunset. This tow may still show the influence of daytime phytoplankton growth. Zooplankton and phytoplankton often undergo diel variations in abundance [Longhurst, 1976; Dam *et al.*, 1993; Cullen *et al.*, 1992; Gardner *et al.*, 1993]. Unless these diel variations in zooplankton depth distributions and net phytoplankton growth are accounted for, day and night P_{dv} and C_p data cannot be compared directly.

To determine if diel variations were evident in either the P_{dv}

or C_p data, we plotted the maximum P_{dv} or C_p concentration from each site versus distance from the coast. The exponential fits in Figures 5a and 5b demonstrate that data from the tow 220 km offshore do not fit the nighttime trend described by the other three tow sites. This tow was collected before the majority of zooplankters had completed their nighttime migration and prior to significant nighttime grazing of the daily phytoplankton growth. We thus refer to the 220 km offshore tow as the "daytime" tow. Based on the exponential fits, the expected nighttime P_{dv} at 220 km is 1.8 times the measured daytime value, while the expected nighttime C_p is 0.7 times the measured daytime value. We apply these scaling factors to the 0- to 30 and 30- to 70-m daytime P_{dv} and C_p data at 220 km for use in comparison to data from the other sites. P_{dv} and C_p data below 70 m were not significantly different between day and night tows so no corrections were made.

P_{dv} and C_p averaged over the tow intervals are significantly correlated both at night (21 mL m⁻², $r^2 = 0.97$, $n = 11$, $p \leq 0.01$) and in the day (9 mL m⁻², $r^2 = 0.98$, $n = 4$, $p \leq 0.01$) (Figure 5c). The similarities between C_p (predominately small phytoplankton) and P_{dv} (predominately large microzooplankton) imply a tight coupling between trophic levels at these sites. Similar correlations between C_p and large size fraction biomass have been observed in the Joint Global Ocean Flux Study (JGOFS) North Atlantic Bloom Experiment [Gardner et al., 1993]. Because P_{dv} and C_p are so tightly correlated at the Multitracers sites, we plot the foraminiferal data against P_{dv} only. Plots of foraminifera versus C_p would convey the same information.

Total Planktonic Foraminiferal Distributions and Biomass

Shells of "living" individuals are easily identified as having protoplasm with or without the aid of Rose Bengal staining. Virtually all foraminiferal shells collected in tows shallower than 200 m are protoplasm-full. The protoplasm of planktonic foraminifera collected in the day tow is generally green-brown. In the night tows, it is yellow to golden-brown, presumably due to nightly degradation of chlorophyll "a" in their symbionts or prey [see Bé and Hamlin, 1967]. The color of *N. dutertrei*, *Globigerinoides ruber*, and *Globoquadrina hexagona* is particularly striking. Their protoplasm in the day tow is bright green in color, presumably from the presence of symbionts or the ingestion of phytoplankters and/or phyto-detritus. Dead specimens of all species are clearly identified by their bone-white, protoplasm-empty appearance. All standing stocks reported here are based on living specimens.

F_{ss} , P_{dv} , and C_p all indicate highest particle concentrations in the cool, subsurface seasonal thermocline (30-70 m) at the site 572 km offshore and in the productive surface water (<30 m) at the other sites (Figure 6). With the exception of the Columbia River plume site (289 km offshore), standing stocks of 125- to 150- μ m foraminifera decrease, while >150- μ m foraminifera increase monotonically offshore. The Columbia River plume site has very few foraminifera relative to the other three sites, particularly in the smaller size fraction. At each station, the depth of the foraminiferal maximum coincides (within the limits of depth averaging) with the depth of the P_{dv} and C_p maxima (Figure 6). However, the ratio of foraminifera to P_{dv} or C_p varies at each site (Figure 7). Relative to P_{dv} , the 121- and 289-km "green" water sites have 4 foraminifera shells mL⁻¹ plankton ($r^2 = 0.97$, $n = 7$, $p \leq 0.01$). In contrast, farther offshore, the 572-km "blue" water site has 36 foraminifera shells mL⁻¹ plankton, almost an order of magnitude greater ($r^2 = 0.84$, $n = 4$). The 220-km site falls between these extremes with 9 foraminifera shells mL⁻¹ plankton ($r^2 = 0.99$, $n = 4$, $p \leq 0.01$).

Species Standing Stock Distributions

We observe a total of 13 foraminiferal taxa in the <200-m samples at the four MOCNESS tow stations (Table 3). We limit our discussion to seven relatively abundant species with clear distribution patterns: *N. dutertrei*, *O. universa*, *G. ruber*, *G. glutinata*, right-coiling *N. pachyderma*, *G. quinqueloba*, and *Globigerina bulloides*. The seven species discussed here account for $93 \pm 9\%$ of the >125- μ m and $95 \pm 8\%$ of the >150- μ m foraminiferal standing stock at the four sites. Total

Table 2. Multiple Opening Closing Net Environmental Sensing System (MOCNESS) Plankton Tow Environmental and Foraminifera Data for Small (125-150 μ m) and Large (>150 μ m) Size Classes

Tow Site, Date, and Time ^a	Depth, m	Volume, m ³	Temp, C	Salt, psu	Density, kg m ⁻³	C_p , m ⁻¹	P_{dv} , mL m ⁻³	Small Count	Large Count	Small, shells m ⁻³	Large, shells m ⁻³
121 km	0-30	33	14.8	32.8	24.3	0.307	8.5	153	105	18.8	12.9
42.060 °N	30-70	39	10.9	33.0	25.2	0.119	2.3	84	40	8.5	4.1
125.665 °W	70-100	114	8.9	33.3	25.8	0.061	0.4	14	20	0.5	0.7
Sept. 21, 1990	100-200	147	8.0	33.8	26.3	0.054	0.5	25	21	0.7	0.6
00:23:00											
220 km	0-30	34	16.3	32.6	23.8	0.230	6.3	105	361	12.4	42.8
42.167 °N	30-70	20	12.2	32.9	24.9	0.128	3.3	37	81	7.4	16.1
126.858 °W	70-100	19	8.9	33.2	25.7	0.058	0.8	2	14	0.4	2.9
Sept. 28, 1990	100-200	113	8.1	33.8	26.3	0.064	0.3	10	34	0.3	1.2
18:27:00											
289 km	0-60 ^{b,c}	57	14.0	32.4	24.1	0.186	5.3	12	205	0.8	14.4
42.169 °N	60-100	40	8.4	32.8	25.5	0.054	1.1	3	26	0.3	2.6
127.694 °W	100-200	99	7.7	33.8	26.4	0.044	0.5	9	14	0.4	0.6
Sept. 23, 1990											
19:24:00											
572 km	0-30	46	17.9	32.6	23.5	0.070	1.1	38	101	3.3	8.9
41.493 °N	30-70	72	11.9	32.7	24.8	0.084	1.7	56	805	3.1	44.7
131.070 °W	70-100	32	8.9	32.6	25.3	0.055	1.1	18	93	2.2	11.6
Sept. 26, 1990	100-200	125	7.5	33.0	25.8	0.031	0.5	44	87	1.4	2.8
23:30:00											

^aPacific Standard Time at start of the 200- to 100-m tow interval.

^bAverage temperature, salinity, density, and C_p for 0-30 m are 16.8°C, 32.3 PSU, 23.5 kg m⁻³, and 0.200 m⁻¹.

^cAverage temperature, salinity, density, and C_p for 30-70 m are 10.4°C, 32.5 PSU, 25.0 kg m⁻³, and 0.143 m⁻¹.

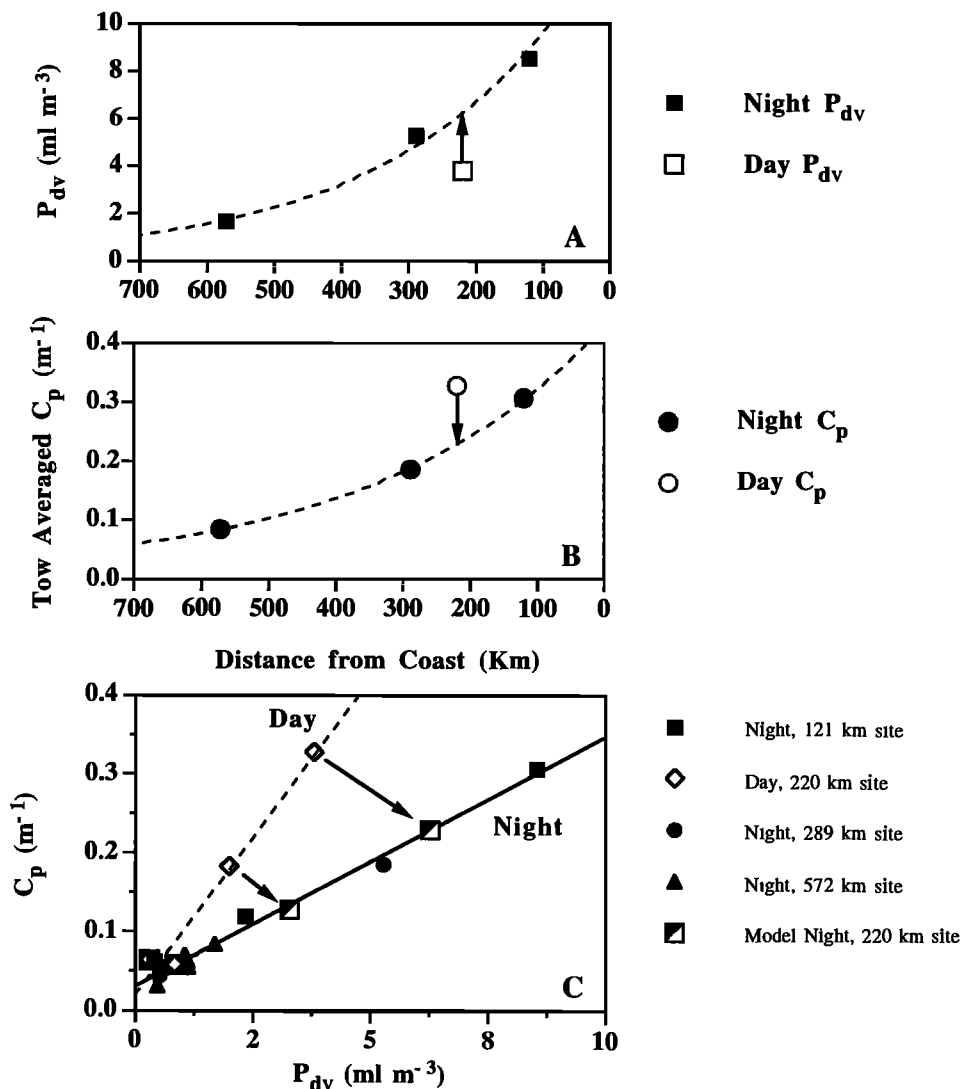


Figure 5. Spatial relationships between (a) maximum nighttime and daytime P_{dv} and (b) maximum nighttime and daytime C_p (averaged over the tow depth intervals) at the four MOCNESS tow sites. The curved lines represent best fit exponential functions to the nighttime P_{dv} and C_p data. (c) The nighttime C_p and P_{dv} data follow a trend with slope of 0.03 mL m^{-2} . The daytime data from the site 220 km offshore follow a relationship with slope of 0.08 mL m^{-2} .

planktonic foraminiferal standing stock $>125 \mu\text{m}$ ranges from 15 to 55 shells m^{-3} (Table 2). Species diversity at the four tow sites is typical of midlatitude sites near oceanic margins [Bé, 1977].

A varimax rotated, Q-mode factor model (Table 4) based on 13 species in all of the MOCNESS samples from 0- to 200-m grouped species with similar distributions. These four factors account for 82% of the information in the $>125\text{-}\mu\text{m}$ percent-maximum normalized data set. Because of the percent-maximum normalization, all species are equally weighted in this analysis. The resulting factors are useful for grouping species with similar distribution patterns, but the information explained by each factor (Table 4) is not proportional to the species' maximum standing stocks (Table 2). Thus comparison of the information explained by each factor is not relevant to a discussion of standing stock distributions.

The seven species listed above group into three of the four faunal factors. The fourth factor is composed of deep-dwelling asymbiotic species. Individuals of these species are sometimes present in the 0- to 200-m samples but are more common in the $>200\text{-m}$ samples [Ortiz, 1995]. We refer to the species associated with these three factors as the "subsurface symbiotic" species (Figure 8), the "shallow symbiotic" species (Figure 9), and the "shallow asymbiotic" species (Figure 10). The terms "shallow," "subsurface," and "deep" derive from the relative depth of the species standing stock maxima at these locations. Use of the terms "symbiotic" and "asymbiotic" derives from the designations of Hemleben *et al.* [1988]. We assume that these groups define assemblages of ecologically similar species.

The "subsurface symbiotic" species (*N. dutertrei* and *O. universa*) both have offshore subsurface maximum at the 572-

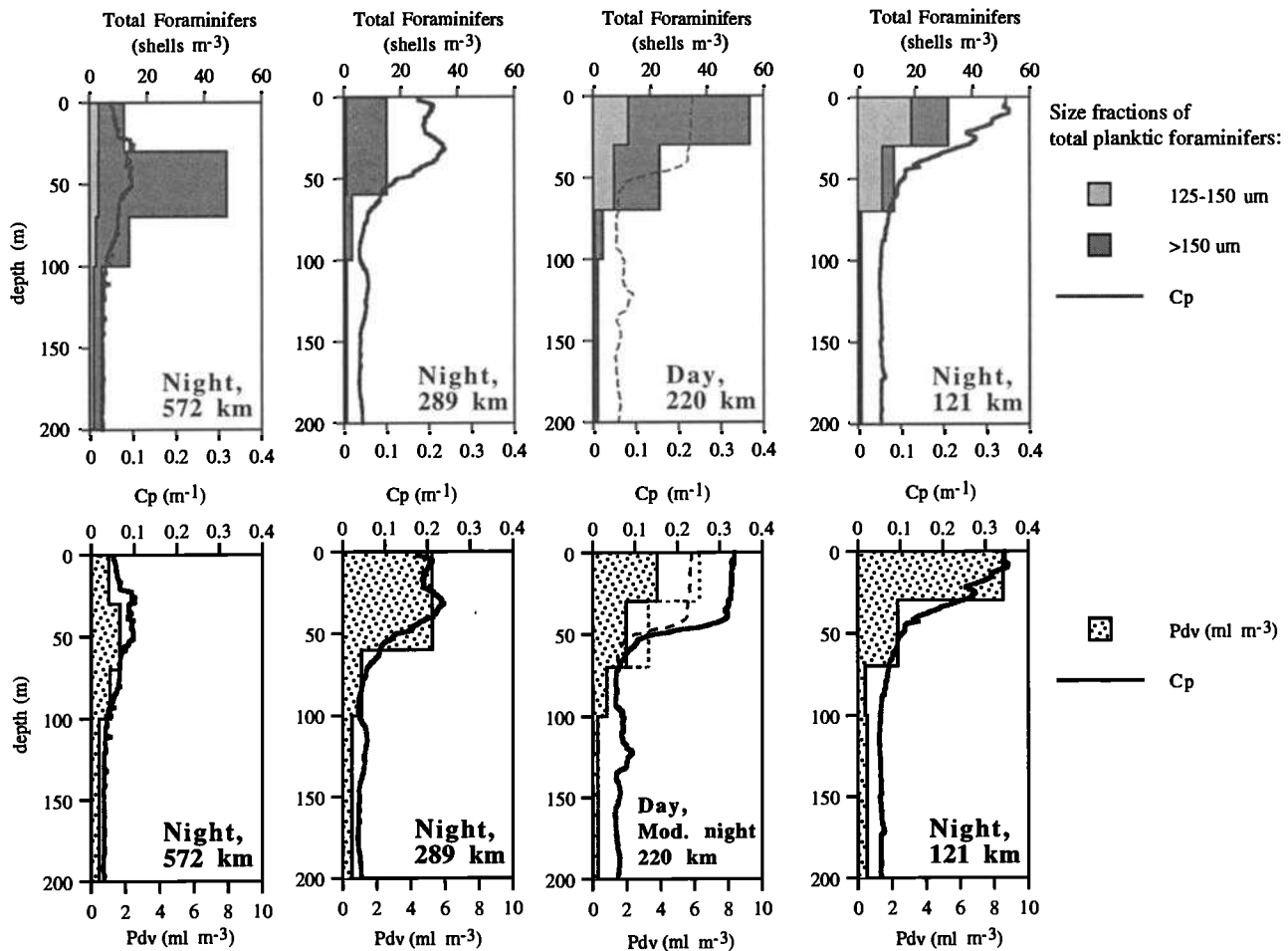


Figure 6. Cumulative histograms of foraminiferal standing stock, plankton displacement volume (P_{dv}), and transmissometer particle attenuation coefficient (C_p) at the four MOCNESS tow sites. Light shading (upper panels) denotes 125- to 150- μm planktonic foraminifera, while heavy shading (upper panels) indicates >150- μm planktonic foraminifera. Dashed lines at the daytime site (220 km offshore) indicate the inferred magnitude of the nighttime P_{dv} and C_p (see Figure 3 and text for details). The C_p data are plotted over the foraminiferal data to demonstrate that the depth of the foraminiferal standing stock maxima at each site is coincident with the particle concentration maxima at each site.

km site and surface maxima at the other locations (Figure 8). Together, these two species account for most of the foraminiferal fauna at the four tow sites and the majority of the >150- μm foraminifera (Table 3). The maximum abundance of these species decreases monotonically toward the coast, with the exception of the Columbia River plume site (289 km offshore), which has too few individuals of either species to fit this general trend. *N. dutertrei* is the most abundant species collected at these sites; *O. universa* was the third most abundant.

The "shallow symbiotic" species consist of *G. ruber* and *G. glutinata*. Although both species are relatively rare in these samples, their distributions are similar (Figure 9). *G. ruber* reaches maximum abundance in the 0- to 30-m sample at the 572- and 220-km sites. *G. glutinata* is most abundant in the 30- to 70-m sample at 220 km and in the 0- to 30-m sample 572 km offshore. The two sites with lowest abundance for these species (121 and 289 km) experience southward flow of

relatively cool, plankton rich waters (Figure 3) which may have excluded these subtropical species.

The "shallow asymbiotic" species (right-coiling *N. pachyderma*, *G. quinqueloba*, and *G. bulloides*) are most common in the cool surface waters of the coastal sites where total biomass is highest (Figure 10). These species are rare in the low-salinity waters of the Columbia River plume (289 km). At the 572-km site they are found from 30- to 100 m in the seasonal and permanent thermocline. Right-coiling *N. pachyderma* and *G. quinqueloba* were the second and fourth most common species in these samples. They accounted for the majority of the 125- to 150- μm foraminifera.

Percent Abundance Comparison Between MOCNESS and Single-Net Tows

Species percent abundance data from the September 1989 and July 1991 single-net tows extend the temporal and

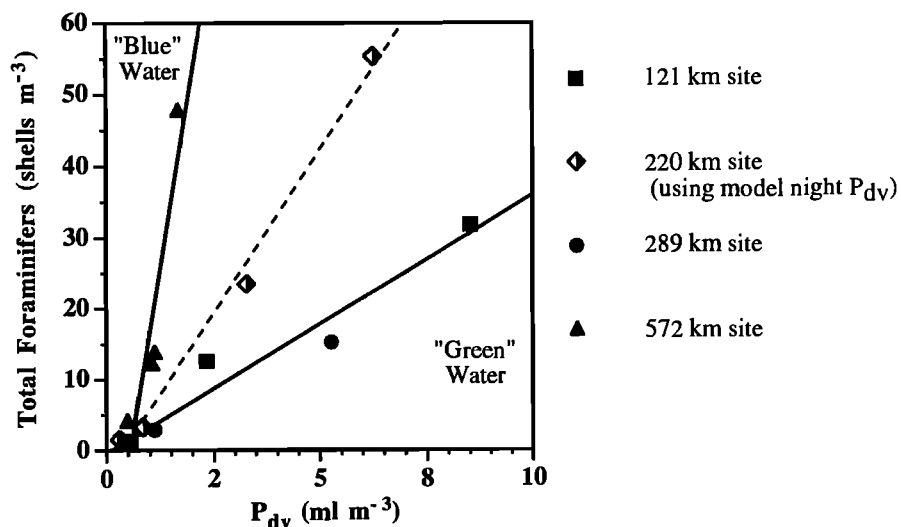


Figure 7. The relationship between planktonic foraminiferal standing stock and P_{dv} . The 220-km foraminifer data are plotted against the model nighttime P_{dv} values. The "green" water sites 121 and 289 km offshore plot along a single line with a shallow foraminifer - P_{dv} slope, while the "blue" water site 572 km site plots along a steep foraminifer - P_{dv} slope. The site 220 km offshore lies between these two extremes.

Table 3. Foraminiferal Species Shells Per Cubic Meter for the 125- to 150- μm Size Class and >150- μm Size Class From September 1990 63- μm Mesh MOCNESS Samples

Site	Depth, m	<i>O. un.</i> ^a	<i>G. ru.</i> ^a	<i>G. aq.</i>	<i>G. ca.</i>	<i>G. bu.</i> ^a	<i>G. di.</i>	<i>G. qu.</i> ^a	<i>N. pa. L</i>	<i>N. pa. R</i> ^a	<i>N. du.</i> ^a	<i>G. sc.</i>	<i>G. me.</i>	<i>G. gl.</i> ^a
125- to 150- μm Size Class														
121 km	0-30	0.0	0.1	0.0	0.0	0.9	0.0	6.3	0.0	9.8	1.6	0.1	0.0	0.0
	30-70	0.0	0.1	0.0	0.0	0.3	0.0	6.3	0.0	1.4	0.4	0.0	0.0	0.0
	70-100	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0
	100-200	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.1	0.0	0.2	0.0	0.0
220 km	0-30	0.0	0.0	0.0	0.0	0.0	0.0	9.0	0.0	3.2	0.2	0.0	0.0	0.0
	30-70	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0	4.4	0.0	0.0	0.0	0.0
	70-100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.2	0.0	0.0
	100-200	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0
289 km	0-60	0.0	0.2	0.0	0.1	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0
	60-100	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.2	0.0	0.0	0.0	0.0
	100-200	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.1	0.0	0.0
	572 km	0-30	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.3	1.9	0.0	0.0
	30-70	0.0	0.1	0.0	0.0	0.0	0.0	0.1	0.0	0.2	2.6	0.0	0.0	0.2
	70-100	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.4	1.6	0.0	0.0	0.1
	100-200	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.7	0.3	0.0	0.0
>150- μm Size Class														
121 km	0-30	1.1	0.1	0.0	0.0	1.2	0.0	0.7	0.1	6.6	2.9	0.0	0.0	0.0
	30-70	0.4	0.0	0.0	0.0	0.0	0.0	1.8	0.0	1.4	0.4	0.0	0.0	0.0
	70-100	0.1	0.0	0.0	0.0	0.1	0.0	0.2	0.1	0.1	0.0	0.1	0.0	0.0
	100-200	0.1	0.0	0.0	0.0	0.1	0.0	0.1	0.1	0.1	0.1	0.1	0.0	0.0
220 km	0-30	13.5	1.8	0.0	0.0	0.1	0.0	1.3	0.1	10.6	14.9	0.0	0.0	0.5
	30-70	1.8	0.8	0.0	0.0	0.2	0.0	4.0	0.0	4.6	4.2	0.0	0.0	0.6
	70-100	0.8	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.6	0.6	0.4	0.0	0.2
	100-200	0.1	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.1	0.1	0.1	0.0	0.0
289 km	0-60	7.7	0.1	0.0	0.3	0.0	0.0	0.0	0.0	0.3	6.0	0.0	0.1	0.1
	60-100	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.8	0.0	0.0	0.0
	100-200	0.4	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
	572 km	0-30	1.0	3.3	0.1	0.0	0.2	0.1	0.0	0.1	0.4	3.4	0.0	0.0
	30-70	15.3	1.7	0.0	0.1	0.0	0.3	0.5	0.1	1.3	25.3	0.0	0.0	0.2
	70-100	1.1	0.1	0.0	0.1	0.0	0.0	0.0	0.0	3.5	6.7	0.0	0.0	0.0
	100-200	0.2	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.8	1.5	0.1	0.0	0.1

Abbreviations are *O. un.*, *Orbulina universa*; *G. ru.*, *Globigerinoides ruber* (White); *G. aq.*, *Globigerinella aequilateralis*; *G. bu.*, *Globigerina bulloides*; *G. di.*, *Globigerinella digitata*; *G. qu.*, *Globigerina quinqueloba*; *N. pa. L.*, *Neogloboquadrina pachyderma* (Left); *N. pa. R.*, *N. pachyderma* (Right); *N. du.*, *N. dutertrei*; *G. sc.*, *Globorotalia scitula*; *G. me.*, *Globorotalia menardii*; and *G. gl.*, *Globigerinella glutinata*.

^a Species discussed in the text.

Table 4. Q-mode Factor Scores for Percent-Maximum Transformed MOCNESS Tow Data (0-200 m)

Taxonomic Grouping	Subsurface Symbiotic Species	Shallow Symbiotic Species	Shallow Asymbiotic Species	Deep Asymbiotic Species
<i>N. dutertrei</i> ^a	0.61 ^a	0.04	0.03	-0.01
<i>O. universa</i> ^a	0.53 ^a	-0.02	0.05	0.02
<i>G. calida</i>	0.47	-0.14	-0.10	0.00
<i>G. menardii</i>	0.25	-0.17	-0.06	0.01
<i>G. ruber</i> ^a	0.12	0.67 ^a	0.11	0.06
<i>G. glutinata</i> ^a	0.03	0.50 ^a	-0.00	-0.00
<i>G. aequilateralis</i>	-0.07	0.42	-0.07	-0.01
<i>G. digitata</i>	0.11	0.23	-0.08	-0.00
<i>G. quinqueloba</i> ^a	-0.07	-0.06	0.80 ^a	0.02
<i>N. pachyderma</i> (R) ^a	0.17	0.02	0.45 ^a	-0.01
<i>G. bulloides</i> ^a	-0.04	-0.09	0.30 ^a	0.03
<i>G. scitula</i>	0.01	-0.11	-0.11	0.75 ^a
<i>N. pachyderma</i> (L)	-0.03	0.09	0.09	0.65 ^a
Information (in %)	17.9%	18.6%	10.3%	35.5%

The four-factor model accounts for 82.3% of the transformed information.

^a These species, which dominate the factor scores, are discussed in the text.

geographic range of our study (Figures 11a, 11c, and 11e; Table 5). These tows show patterns similar to the September 1990 tows (Figures 11b, 11d, and 11f). Shallow asymbiotic species are abundant near the coast, while shallow and subsurface symbiotic species are more abundant offshore. The offshore transition from asymbiotic to symbiotic dominance appeared sharper in September 1989 than in September 1990. Right-coiling *N. pachyderma* and *G. quinqueloba* each accounted for ≈20% of the offshore fauna in September 1989 (Figure 11a), and ≈10% of the fauna during September 1990 (Figure 11b). In the high-biomass coastal upwelling zone within 100 km of the coast, *G. bulloides* was the dominant planktonic foraminifera (Figure 11a). The subsurface symbiotic species (*O. universa* and *N. dutertrei*) were less abundant offshore in September 1989 (Figure 11c) than in September 1990 (Figure 11d). The shallow symbiotic species (*G. ruber* and *G. glutinata*) had similar distribution patterns in the two years (Figures 11e and 11f), but the relative dominance of the two species switched between years.

Species Maxima, Environmental Variability, and Size Changes

G. ruber was the only species to demonstrate a clear distribution trend as a function of temperature. This species

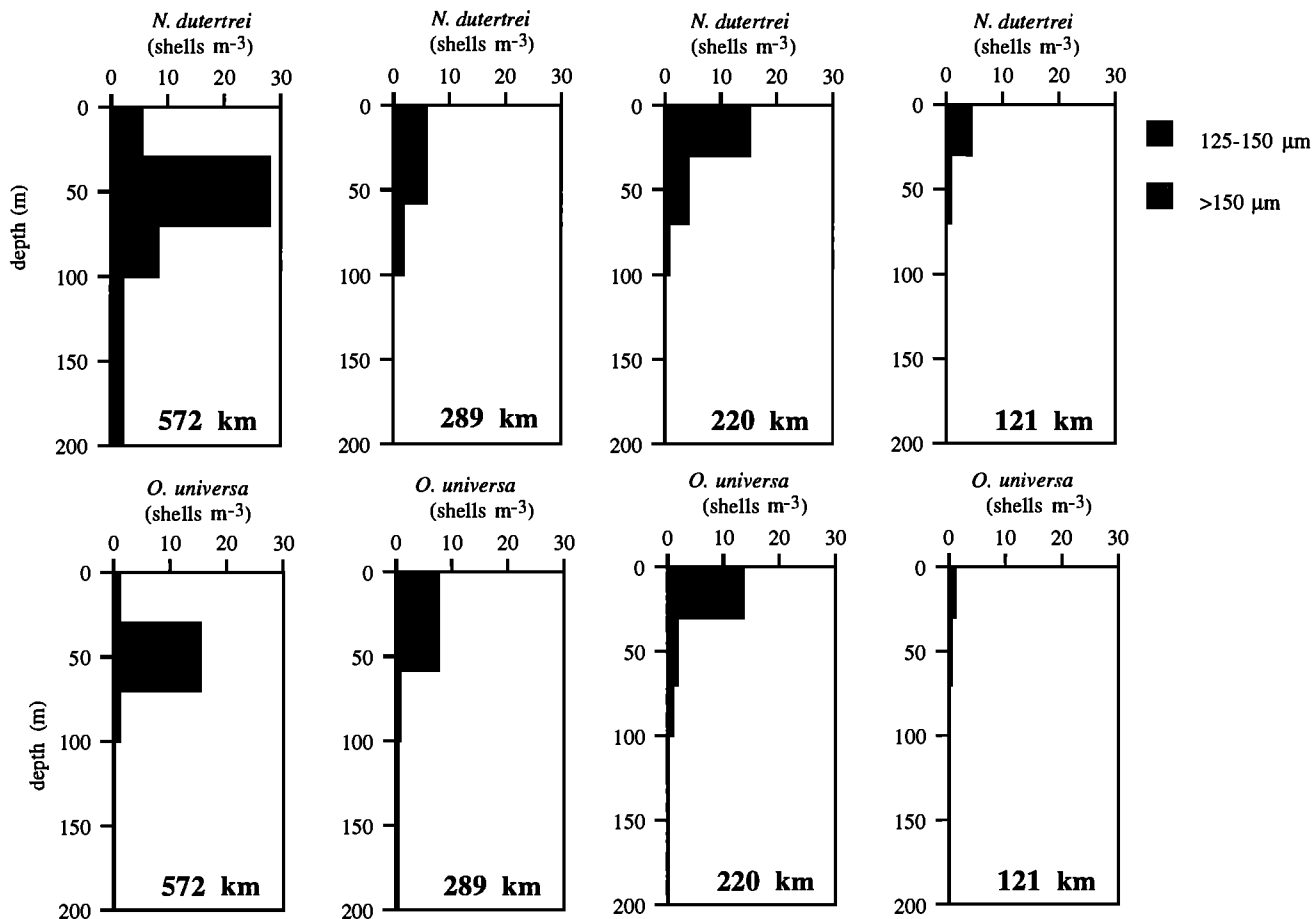


Figure 8. Cumulative histograms of the subsurface symbiotic planktonic foraminifera *N. dutertrei* and *O. universa* at the four MOCNESS tow sites. Heavy shading denotes small planktonic foraminifera (125-150 μm), while light shading indicates larger foraminifera (>150 μm). These species are most common in the offshore thermocline and exhibit surface maxima at the other sites.

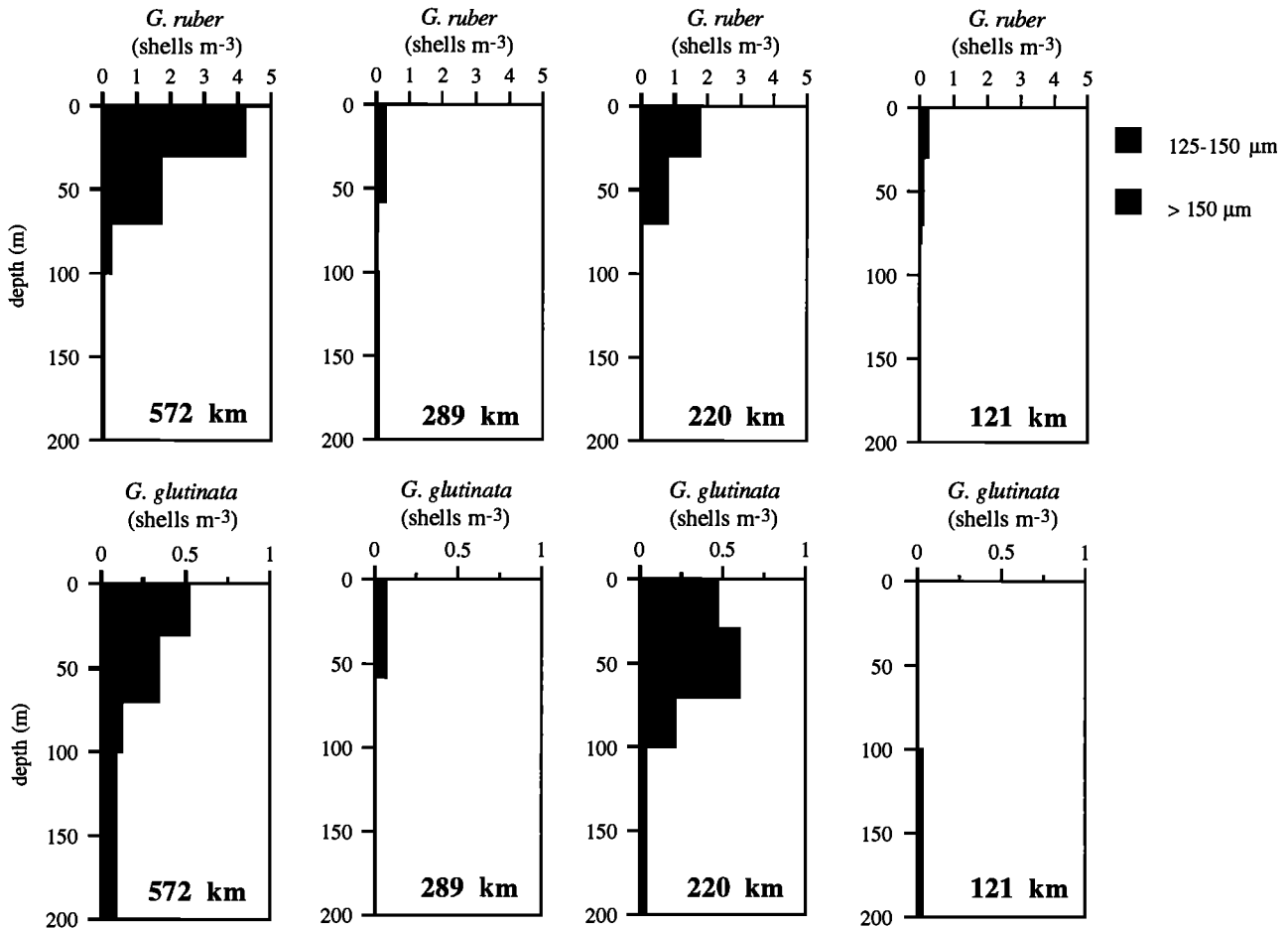


Figure 9. Cumulative histograms of the shallow symbiotic planktonic foraminifera *G. ruber* and *G. glutinata* at the four MOCNESS tow sites. Shading is as in Figure 6. These species are most common in the warm surface waters 572 km offshore and in the northward flowing waters 220 km offshore.

decreased in abundance with decreasing temperature and is very rare in waters of less than 15°C (Figure 12b). None of the other species demonstrated any statistically significant or physiologically meaningful standing stock variations with respect to temperature or salinity in these samples (Tables 2 and 3; Figures 12a, 12b, and 12c). *O. universa*, *N. dutertrei* (Figure 12a), and *G. glutinata* (Figure 12b) have minimum standing stock near 15°C and higher standing stocks toward both temperature extremes. Right-coiling *N. pachyderma*, *G. quinqueloba*, and *G. bulloides* (Figure 12c) had patterns which were equally complex. The coarse resolution (0-60 m) sample at the site 289 km offshore does not greatly affect these results. The average temperature from 0- to 60 m at this site is 14.0°C. The average temperature from 0- to 30 m is 16.8°C. Assuming foraminiferal standing stock is proportional to C_p , the 0- to 60-m average underestimates 0- to 30-m foraminiferal standing stock by $\approx 10\%$, which is less than the 20% measurement error (see: Comparisons of P_{dv} and C_p). Plotting the foraminiferal data at 16.8°C, rather than 14.0°C, would not alter the basic structure of these results.

The shape of the observed distribution patterns with respect to temperature is unlike the gaussian distribution patterns expected based on each species' optimum temperature as

defined by large-scale plankton tow studies [Bé, 1977; Bé and Hutson, 1977] and laboratory culture experiments [Bijma et al., 1990b]. It thus seems likely that factors other than temperature are heavily influencing the distributions of these species at these sites.

In contrast, the relationships between the standing stock maxima for each species at each site and zooplankton biomass (P_{dv}) are physiologically plausible (Figures 12d, 12e, and 12f). The shallow symbiotic species (Figures 12d and 12e) have highest concentration in low-biomass, less turbid offshore waters. These species decrease in abundance as biomass and water turbidity increase. For comparison, the shallow asymbiotic species (Figure 12f) are most abundant in the high-biomass, high-turbidity water near the coast. *G. bulloides* was the least common of the three shallow asymbiotic species. This species decreases rapidly between 9 and 5 mL m⁻³ and is essentially absent below P_{dv} values of 5 mL m⁻³. Right-coiling *N. pachyderma* decreased rapidly below P_{dv} values of 6 mL m⁻³. *G. quinqueloba* had roughly constant standing stock over a large range of P_{dv} values then dropped rapidly in standing stock when P_{dv} fell below 2 mL m⁻³.

Shell size in *O. universa* and *N. dutertrei* increases offshore (Table 6). Increasing mean shell size is positively correlated

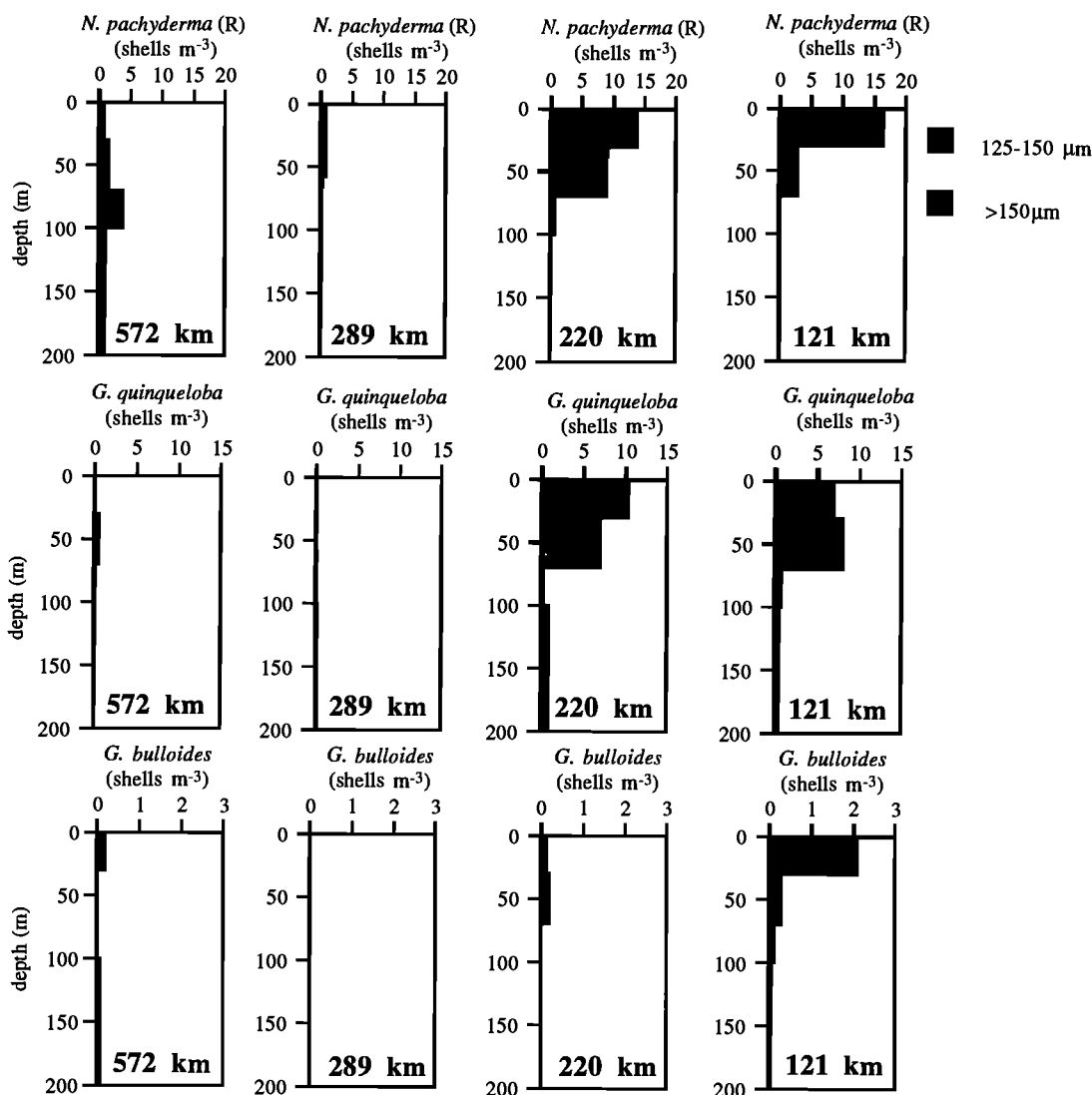


Figure 10. Cumulative histograms of the shallow asymbiotic planktonic foraminifera right-coiling *N. pachyderma*, *G. quinqueloba*, and *G. bulloides* at the four MOCNESS tow sites. Shading is as in Figure 6. Asymbiotic species are most common in high-biomass waters near the coast and decrease offshore.

with standing stock (Figure 13a) for *O. universa* ($r^2 = 0.65$, $n = 4$) and *N. dutertrei* ($r^2 = 0.44$, $n = 4$). Size changes in these species (Figure 13b) are inversely correlated with increasing plankton biomass as measured by P_{dv} ($r^2 = 0.96$, $n = 4$, $p \leq 0.05$ and $r^2 = 0.86$, $n = 4$). In contrast, right-coiling *N. pachyderma* shells do not vary significantly in size across the transect (Table 6). Changes in the size of right-coiling *N. pachyderma* are uncorrelated with either changes in its standing stock (Figure 13a) or changes in P_{dv} (Figure 13b).

Discussion

We have tested for relationships between living foraminiferal standing stock and size against light availability, planktonic biomass (P_{dv} and C_p), temperature, and salinity. These data suggest that while temperature is the dominant control on a species distribution near the limits of its thermal tolerance, food and light may provide the primary

control under favorable thermal conditions. Because the MOCNESS plankton tows used for this purpose were collected at different sites over a span of only 7 days, we cannot address the possible role of lunar cyclicity on the standing stock and size changes we observe [Hemleben *et al.*, 1988; Bijma *et al.*, 1990a; Erez *et al.*, 1991]. However, minimum and maximum standing stock and size in these samples are not correlated with the timing of the full or new moon at our sites. Longer records from midlatitude sites with better temporal resolution are necessary to address this topic.

With the exception of *G. ruber*, temperature does not play a dominant role in determining the mesoscale distribution of planktonic foraminifera at the sites we studied. During September 1990, *G. ruber* decreases in abundance with decreasing temperature and is essentially absent from waters of $<15^\circ\text{C}$. *G. ruber* was absent in September 1989 when mixed layer temperatures averaged $\approx 2^\circ\text{C}$ cooler. The 14° isotherm marks the northern limit of its distribution in plankton tows

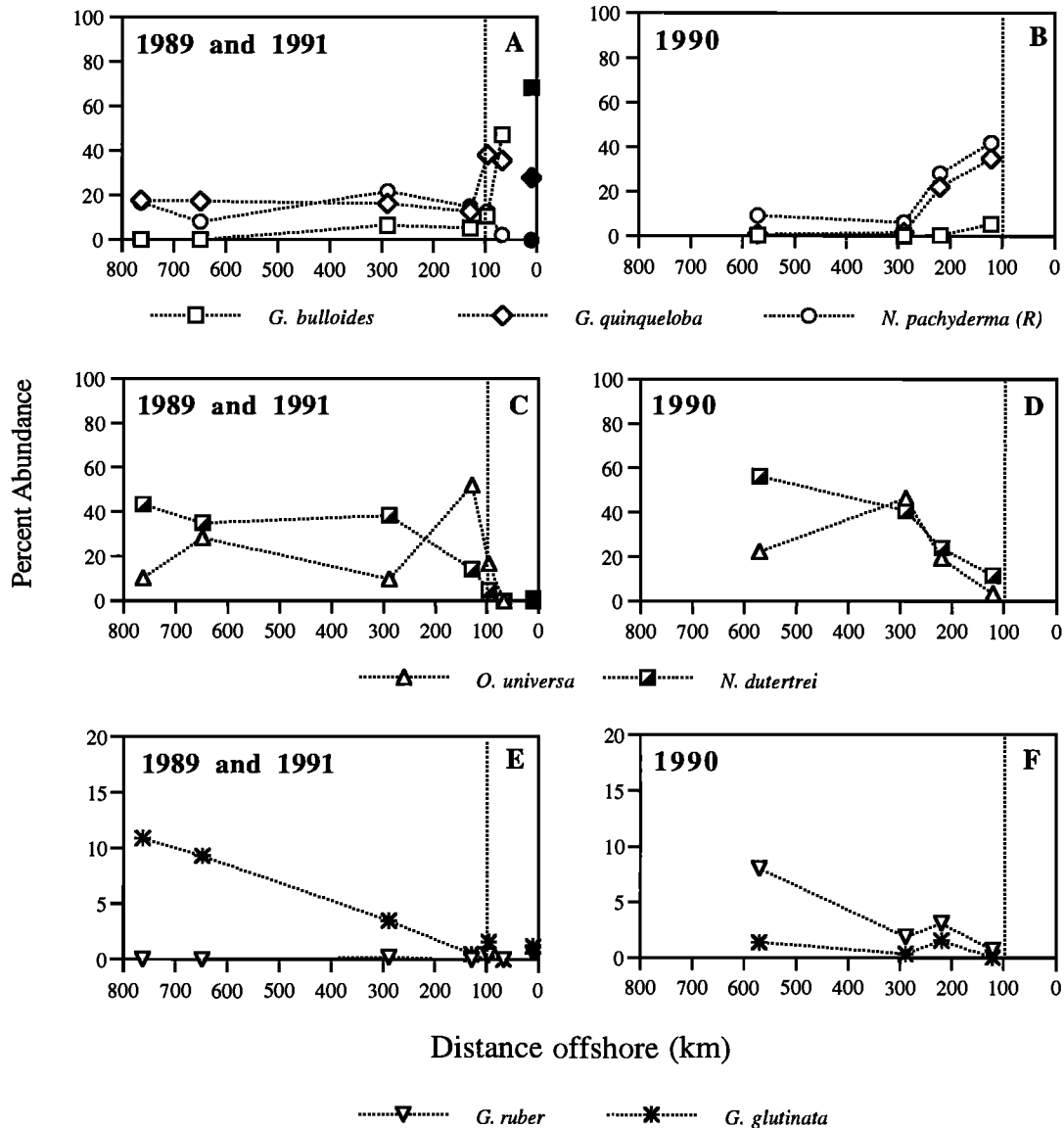


Figure 11. Species percent abundance (>125 μm) across the Multitracers transect during the upwelling season in 1989, 1990, and 1991. The 1989 and 1991 data (Figures 11a, 11c, and 11e) are from single-net plankton tows: all sites >67 km offshore were collected in September 1989. The tow data 10 km offshore (solid symbols in Figures 11a, 11c, and 11e) were collected in July 1991. Note high abundance of *G. bulloides* within 100 km of coast. The 1990 data (Figures 11b, 11d, and 11f) are 0- to 200-m integrated MOCNESS samples. Vertical lines at 100 km mark the most coastal station from 1990, for comparison to 1989 and 1991 tow locations. Species groupings are shallow asymbiotic species (Figures 11a and 11b), subsurface symbiotic species, (Figures 11c and 11d), and shallow symbiotic species (Figures 11e and 11f).

[Bé and Tolderlund, 1971; Bé and Hamlin, 1967] and its lower thermal limit in the laboratory [Bijma et al., 1990a]. Our field results agree that *G. ruber* does not succeed at temperatures <14°C.

Effect of Food and Light on Species Distributions

Comparison of total foraminiferal standing stock to the P_{dv} data (Figure 6) indicates two biological provinces in the waters we study, coastal upwelling influenced "green" waters that have low foraminifera to biomass ratios and offshore "blue" waters that have higher foraminifera to biomass ratios.

The foraminiferal faunas in the "green" sites are dominated by asymbiotic foraminifera, while foraminifera with algal symbionts flourish in the "blue" waters offshore. These two faunal provinces reflect the physical and biological changes that occur as one traverses the coastal transition zone (CTZ). During the upwelling season, increasing particle load toward the coast is associated with a factor of 2 decrease in the depth of the 1% PAR light level from ≈ 70 m offshore to ≈ 35 m near the coast. As a result, shallow dwelling foraminifera near the coast can experience lower light levels than deeper dwelling individuals in the offshore thermocline.

Table 5. Foraminiferal Species Percent Abundance for the >125-µm Size Class From Seven 1989 and 1991 63-µm Mesh Single-Net Tows

Distance and Date	Latitude Longitude	Depth, m, and Time ^a	% <i>O. un.</i> ^b	% <i>G. ru.</i> ^b	% <i>G. aq.</i>	% <i>G. ca.</i>	% <i>G. bu.</i> ^b	% <i>G. di.</i>	% <i>G. qu.</i> ^b	% <i>N. pa.</i> ^b	% <i>N. pa.</i> ^b	% <i>N. pa.</i> ^b	% <i>N. du.</i> ^b	% <i>G. sc.</i>	% <i>G. me.</i>	% <i>G. gl.</i> ^b	% Other
10 km	44.652°N	0-20 m	0.0	0.6	0.0	0.0	68.5	0.0	28.0	0.6	0.0	0.0	1.2	0.0	0.0	1.2	0.0
July 23, 1991	124.177°W	10:00															
67 km	42.283°N	0-100 m	0.0	0.0	0.0	0.0	47.3	0.0	35.7	13.7	2.2	0.0	0.0	1.1	0.0	0.0	0.0
Sept. 15, 1989	124.931°W	00:50															
97 km	42.103°N	0-200 m	16.7	0.4	0.0	0.0	10.6	0.0	38.2	7.3	12.6	4.9	4.9	0.0	0.0	1.6	2.8
Sept. 17, 1989	125.363°W	02:26															
129 km	42.033°N	0-70 m	52.0	0.0	0.0	0.0	5.4	0.0	12.8	0.0	15.0	14.3	0.0	0.0	0.0	0.5	0.0
Sept. 16, 1989	125.754°W	01:28															
289 km	42.174°N	0-200 m	9.9	0.2	0.0	0.0	6.6	0.0	16.3	1.7	21.8	38.4	0.7	0.0	0.0	3.5	1.1
Sept. 24, 1989	127.611°W	03:18															
649 km	41.555°N	0-160 m	28.5	0.0	0.0	0.2	0.0	0.0	17.3	1.6	8.1	35.0	0.0	0.0	0.0	9.3	0.0
Sept. 20, 1989	132.012°W	00:00															
763 km	41.268°N	0-160 m	10.3	0.0	0.0	0.4	0.0	0.0	17.6	0.1	16.7	43.3	0.0	0.0	0.0	10.9	0.7
Sept. 21, 1989	133.341°W	03:46															

Abbreviations are *O. un.*, *Orbulina universa*; *G. ru.*, *Globigerinoides ruber*; *G. aq.*, *Globigerinella aequilateralis*; *G. bu.*, *Globigerina bulloides*; *G. di.*, *Globigerinella digitata*; *G. qu.*, *Globigerina quinqueloba*; *N. pa. L.*, left-coiling *Neoglobobulimina pachyderma*; *N. pa. R.*, right-coiling *N. pachyderma*; *N. du.*, *N. dutertrei*; *G. sc.*, *Globobulimina scitula*; *G. me.*, *Globobulimina menardii*; and *G. gl.*, *Globigerinita glutinata*. Percentages may add to greater than 100 due to rounding.
^aLocal Pacific Standard Time.
^bValues correspond to species discussed in text.

The depth of the maximum in foraminiferal standing stock and plankton biomass (F_{ss} , P_{dv} , and C_p ; Figure 6) also depends on the biophysical environment. At the 121-km site, where the Cape Blanco filament supplies nutrient-rich turbid waters from coastal upwelling sites, plankton biomass and foraminiferal standing stock are concentrated near the surface (0- to 30-m net; Figure 6). In contrast, plankton biomass and foraminiferal standing stock at the relatively clear water, oligotrophic site 572-km offshore is concentrated in the thermocline (30- to 70-m net), near the major source of new nutrients at this location.

We infer that the foraminiferal concentrations and size changes in these waters arise from the different responses of asymbiotic and symbiotic foraminifera to changes in food and light. At these study sites, asymbiotic foraminiferal standing stock is positively correlated with increasing biomass, a measure of greater potential food. This implies asymbiotic foraminifera become increasingly food-limited as biomass decreases.

In the laboratory, all species of planktonic foraminifera will accept prey of various types [*Hemleben et al.*, 1988, and references therein]. However, prey ingestion alone cannot explain the standing stock and size distribution of the symbiotic species. If food were limiting their standing stocks and size at these sites, we would observe increasing standing stock and size with increasing plankton biomass. In fact, their standing stocks decrease with increasing plankton biomass and increase with increasing ambient light. We thus infer these symbiotic species gain additional nutrition from their symbionts as light levels increase offshore into lower biomass waters. Consistent with our field observations, published culture work demonstrate that endosymbionts can provide an important source of nutrition to foraminiferal hosts [*Bé et al.*, 1981, 1982; *Spero and Parker*, 1985; *Jørgensen et al.* 1985].

Our findings suggest a physiological explanation for why asymbiotic species can outcompete symbiotic species in high-biomass waters and vice versa. *Berger* [1969] observed that planktonic foraminifera are less abundant in high-biomass coastal sites than in the open ocean. Because our study demonstrates asymbiotic species increase in abundance with increasing coastal biomass, we infer light limitation of symbiotic species may be the cause of the lower total foraminiferal standing stocks in coastal waters. Where light is abundant, at lower latitude and where waters are less turbid, symbiotic foraminiferal standing stock and size increase, while asymbiotic foraminiferal standing stock decreases.

At plankton biomass levels below those measured at the 572-km site in this study, symbiotic foraminifera may become limited by some variable other than light. If food were the limiting agent, this would result in a decrease in symbiotic species size and standing stocks at very low biomass, high light sites. This seems to be the case in the central equatorial Pacific along 140°W at sites that are more oligotrophic than the Multitracers sites [*Watkins et al.*, 1995]. During sampling, temperature at these low latitude sites was nearly constant, the foraminiferal community was dominated by symbiotic species, and both symbiotic and asymbiotic foraminifera were associated with increasing plankton biomass. Another recent foraminiferal study in the eastern

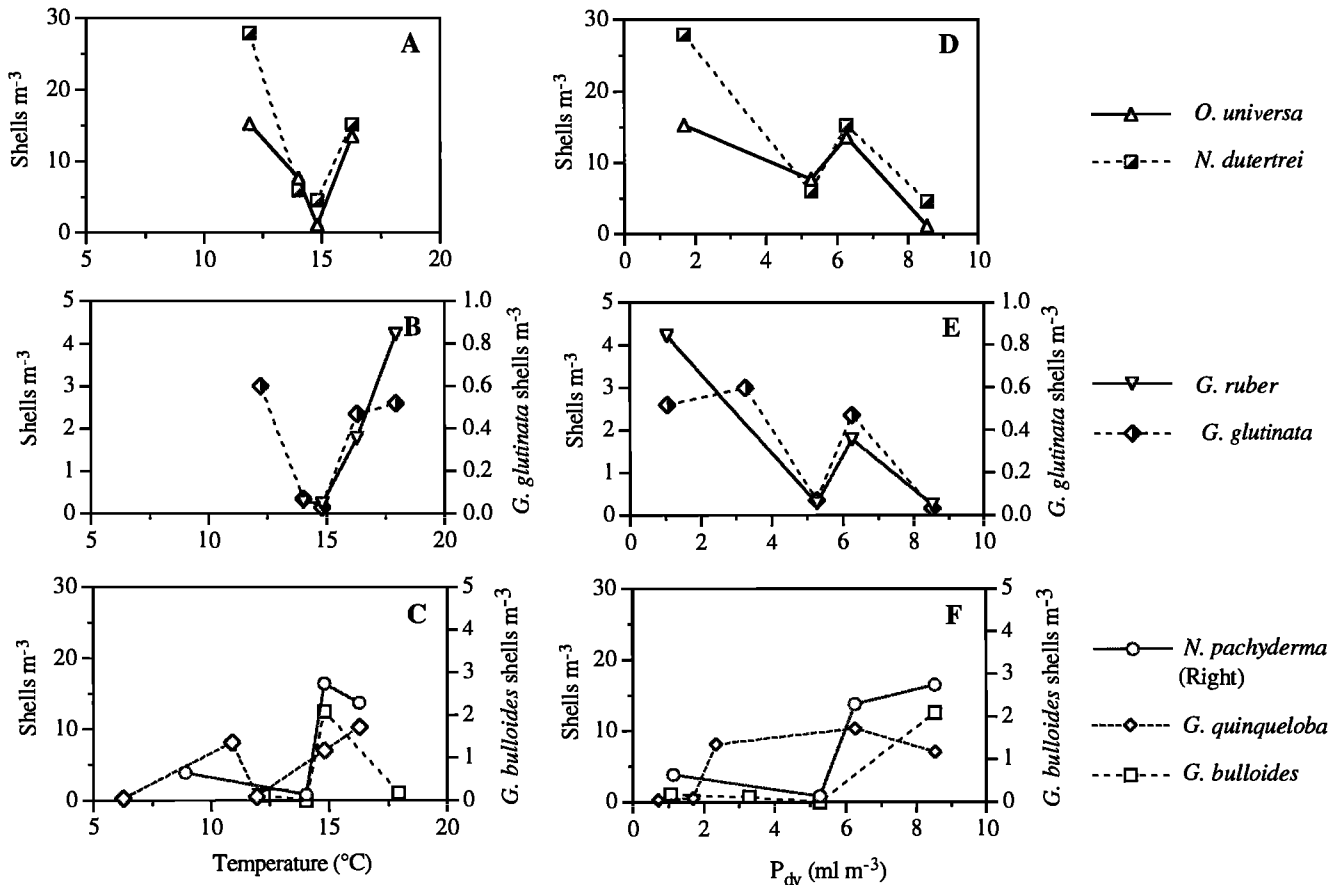


Figure 12. Planktonic foraminiferal standing stock versus temperature and P_{dv} . (a-c) *G. ruber* is the only species to demonstrate a clear relationship to temperature. (d-e) Symbiotic species decrease with increasing P_{dv} , (f) while asymbiotic species increase with P_{dv} . Measurement errors of 20% apply for foraminiferal standing stock and P_{dv} .

equatorial Atlantic linked high foraminiferal standing stocks to intermediate levels of phytoplankton biomass [Oberhänsli *et al.*, 1992]. These researchers found foraminiferal concentration decreased both toward high-biomass, coastal upwelling sites and toward lower-biomass, open-ocean, oligotrophic sites. We suggest that the offshore decrease toward oligotrophic conditions observed by Oberhänsli *et al.* [1992] arises from food limitation of both symbiotic and asymbiotic species, while the onshore decrease toward high-biomass coastal sites arises from light limitation of symbiotic species. If this interpretation is correct, our inference of light limitation at the midlatitude Multitracers sites may extend to turbid continental margins in the tropics as well.

Table 6. Mean Individual Size of Selected Species From the MOCNESS Tows

Distance Offshore, km	<i>O. universa</i> Size	<i>N. dutertrei</i> Size	Right-coiling <i>N. pachyderma</i> Size
121	343 ± 83 (12)	236 ± 31 (41)	202 ± 26 (168)
220	441 ± 53 (107)	342 ± 79 (121)	218 ± 30 (121)
289	493 ± 89 (110)	403 ± 78 (79)	213 ± 38 (12)
572	576 ± 53 (153)	434 ± 63 (201)	231 ± 30 (32)

Mean size (± one standard deviation) is given in microns. Number of shells measured is listed in parenthesis.

Accounting for differences between symbiotic and asymbiotic species may resolve the apparent conflict discussed by Thunell and Sautter [1992] as to whether *N. dutertrei* should reach maximum seasonal abundance in upwelling zones earlier or later than *G. bulloides*. Kroon and Ganssen [1989], working on pump samples from the northern Indian Ocean, suggest that the standing stock maximum of *N. dutertrei* should lead that of *G. bulloides*, because *N. dutertrei* feeds primarily on phytoplankters that peak in abundance before the zooplankters on which *G. bulloides* feeds. Thunell and Sautter [1992] observed the opposite pattern in the San Pedro Basin off California. They explain this apparent conflict in terms of hydrographic variability between the two regions and suggest that *N. dutertrei* prefers a thermally stratified water column with a pronounced chlorophyll maximum. We argue that asymbiotic *G. bulloides* reaches maximum abundance in turbid waters at times of greatest food availability, while symbiotic *N. dutertrei* can only reach high standing stocks and largest size in lower-turbidity, lower-biomass waters. Our explanation of this pattern differs from that of Thunell and Sautter [1992] or Kroon and Ganssen [1989] who stress the importance of herbivory on the distribution of *N. dutertrei* rather than the light needs of its endosymbionts as we suggest.

Our conceptual model of food and light limitation expands upon the current paradigm of planktonic foraminiferal dietary

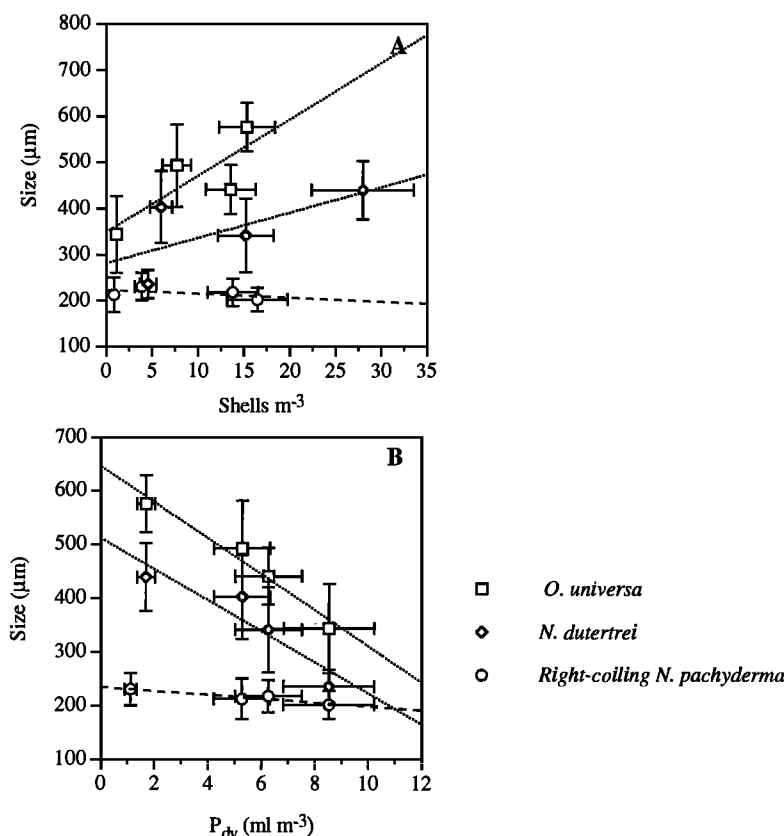


Figure 13. Relationships between foraminiferal size, standing stock, and P_{dv} . Two symbiotic species (*O. universa* and *N. dutertrei*) demonstrate (a) positive correlation between size and standing stock and (b) significant negative correlations between size and P_{dv} . Increasing values of P_{dv} imply more turbid water. The asymbiotic species, right-coiling *N. pachyderma*, does not demonstrate significant correlation between size and standing stock or size and P_{dv} .

needs by synthesizing field and laboratory results. Much of the nutritional needs of these species are met through omnivorous feeding habits [Hemleben *et al.*, 1988]. Previous MOCNESS studies from open-ocean sites using 333- μm mesh nets stress the linkage between species distribution and food, demonstrated by the presence of foraminifera at the DCM [Fairbanks *et al.*, 1979; Fairbanks and Wiebe, 1980; Ravelo *et al.*, 1990; Bé *et al.*, 1985]. Our added contribution is to evaluate the interaction of food and light as factors contributing to the nutrition of foraminiferal species and to assess their impact on species distribution patterns in the mid-latitudes.

Food Threshold for Asymbiotic Species

The low concentrations of *G. bulloides* 121 km offshore in the California Current are somewhat surprising given the affinity of this species for cold, productive coastal upwelling zones [e.g., Cullen and Prell, 1984; Curry *et al.*, 1992; Thunell and Sautter, 1992; Thiede and Jünger, 1992]. Low concentrations in the MOCNESS plankton tows >121 km offshore are consistent with this species' rarity in a yearlong sediment trap time series from the same sites [Ortiz and Mix, 1992]. However, in the September 1989 and 1991 tows, *G. bulloides* are encountered in high percent abundance inshore of 100 km at the high-biomass sites closest to the zone of

active upwelling (Figure 11a). What prevents *G. bulloides* from thriving farther offshore? We suggest that the low offshore concentrations of *G. bulloides* arise from food limitation. The distribution of this species serves as an extreme example of a process common to all three of the asymbiotic species we studied.

We propose that asymbiotic species have different critical food thresholds below which each is absent. Based on the MOCNESS standing stock data (Figure 13), these presumed food needs were greatest for *G. bulloides* (the least abundant of the three asymbiotic species), followed by right-coiling *N. pachyderma*, and finally *G. quinqueloba*. Hemleben *et al.* [1988] report that *G. quinqueloba* harbors crysophycophyte symbionts. These symbionts are similar to those of *Globigerinella aequilateralis* and do not appear to contribute as much to host nutrition as do dinoflagellate symbionts [Faber *et al.*, 1988; 1989]. This explains why the distribution of *G. quinqueloba* in this study bears greatest resemblance to asymbiotic species. The small contribution to host nutrition provided by the crysophycophyte symbionts could, however, explain why *G. quinqueloba* survives at lower food concentrations than right-coiling *N. pachyderma* and *G. bulloides*.

Effects of Food and Light on Shell Size

The observed correlations between shell size, standing stock, and P_{dv} for *O. universa* and *N. dutertrei* (Figure 13) are

consistent with laboratory culture work on symbiotic photosynthesis [Spero, 1992; Bijma et al., 1992]. These laboratory studies demonstrate that symbiotic foraminifera grown under high light conditions reach larger size than individuals grown under low light conditions. Additional laboratory studies show that the symbiotic foraminifer *G. sacullifer* reaches larger adult size when well fed and under high light conditions [Bé et al., 1981; 1982; Caron et al., 1981; Caron and Bé, 1984]. Our field data imply that larger individuals of the subsurface symbiotic species are associated with higher light conditions (as inferred from lower P_{dv}) and with abundant, thriving populations as measured by their species' standing stock.

In contrast, the standing stock and species percentages of asymbiotic species increase with food availability. Despite this positive correlation, right-coiling *N. pachyderma*, the most abundant of the asymbiotic species, maintains a constant size as food increases (Figure 12). This suggests that feeding rate does not provide a strong control on calcification rate in asymbiotic foraminifera. Similarly, other asymbiotic calcifying organisms (e.g., mollusca, benthic foraminifera, and cnidaria) generally calcify more slowly than related, symbiotic counterparts [Jones et al., 1988, and references therein]. Comparing symbiotic and asymbiotic species, we infer that food availability does not radically alter calcification rate but that symbiont activity does through modification of the carbonate chemistry at the site of calcite deposition.

Asymbiotic Species at the Low-Salinity Site: Salinity Limits or Advection?

Despite the lack of a clear pattern between asymbiotic species standing stock and salinity, their conspicuous absence from the low-salinity Columbia River plume site 289 km offshore (Figure 10) suggests either (1) secondary control by a low-salinity threshold or (2) physical exclusion from the plume by the hydrographic front associated with the Cape Blanco filament (Figures 2 and 3d). We compare the observed salinity of the plume (≈ 32.3 psu, Figure 3) with low-salinity thresholds for each species. The low-salinity threshold was determined from the species' salinity optimum and standard deviation reported by Bé [1977]. Bé [1977] defined the salinity optimum for each species based on the mean sea surface salinity at the location of the species' maximum standing stock using data from over 150 plankton tows (0-200 m). We assume that a species low-salinity tolerance is 1 standard deviation below its optimum. All three species have salinity thresholds lower than the salinity of the Columbia River plume: *N. pachyderma* (34.1 ± 2.9 psu, $-1\sigma = 31.2$ psu), *G. quinqueloba* (34.5 ± 3.6 psu, $-1\sigma = 30.9$ psu), and *G. bulloides* (34.8 ± 5.1 psu, $-1\sigma = 29.7$ psu). This suggests that low salinity was not responsible for their absence from the plume.

Lagrangian drifter studies of filaments in the California Current demonstrate that these dense, cold, and saline features subduct under less dense offshore surface waters, or entrain them, rather than diffuse into warmer, fresher, surface waters [Paduan and Niiler, 1990; Swenson et al., 1992]. Our plankton tows suggest that the asymbiotic planktonic foraminifera inhabiting these filaments record much the same pattern, with exclusion from the less dense Columbia River

plume and a deep (70-100 m), potentially subducted distribution 572 km offshore than at sites inshore of 220 km. Another California Current plankton tow study found similar species distribution patterns among a dolioidid, a calanid, and juvenile euphausiids [Mackas et al., 1991]. They attribute the offshore deepening of these species' maxima to filament subduction [Hofmann et al., 1991].

While the physical exclusion argument may explain both the low abundance of asymbiotic foraminifera in the high-biomass waters of the Columbia River plume and their deeper distribution at the 572-km site, we cannot entirely exclude the direct effects of low salinity on the foraminiferal distributions in the plume. This is because the abundant and shallow symbiotic species which presumably become entrained into the plume from the offshore side and the south also decrease in abundance within it. *O. universa* and *N. dutertrei* either are not as adversely affected by low salinity as other species of planktonic foraminifera or are not excluded as effectively, because the dense, cold, and salty filaments associated with the upwelling front are not found on the offshore side of the plume.

Implications for Paleoceanographic Studies

Mix [1989a, b] suggested that temperature and oceanic productivity (through their influence on respiration rate and available food) were the dominant variables recorded in the foraminiferal fossil record. He further suggested that because these two processes were uncorrelated at large spatial scales, it was possible to reconstruct the basin-scale features of both environmental factors through statistical transfer functions using the same foraminiferal calibration data set. We have not compared our foraminiferal data directly to primary productivity rate measurements, but the Multitracers sites are located in a region where changes in biomass and ambient light are often tightly linked to variations in oceanic primary productivity. The results of our study indicate physiological linkages between foraminiferal species composition and variations in ambient light and available food driven by changes in oceanic productivity. While the statistical model employed by Mix [1989a, b] did not specifically incorporate any biological processes, our study supports its basic assumptions and suggests ways to improve such models by considering symbiotic and asymbiotic foraminifera separately and by including shell size information.

It is useful to consider the MOCNESS plankton tow data in terms of percent abundance because this is the form of data most easily accessible from the sediments (Figure 11). Comparison of the 1989 and 1991 data with the 1990 percent data yields essentially the same foraminiferal distributions: shallow asymbiotic species are most abundant near the coast, while symbiotic species are most common offshore. We argue that the same environmental factors (food and light) are responsible for the structure of the foraminiferal community during the 1989 and 1990 upwelling seasons. The increase in percent abundance of asymbiotic species (and thus decrease of symbiotic species) in the offshore fauna during 1989 (Figure 11a) was accompanied by a doubling of the offshore particle standing stock as measured by C_p (Figure 4). The increase in particle concentration was also associated with a 2°C cooling. This cooling was sufficient to eliminate *G. ruber* from the 1989 fauna because this species is near the limit of its thermal

tolerance at these sites. Based on the MOCNESS results from September 1990 (Figure 13), it is unlikely the 2°C cooling was responsible for the asymbiotic species increase and symbiotic species decrease during September 1989. If these distribution patterns are recurrent features of the high-flux upwelling season, the factors that give rise to them should leave traces in the sedimentary record. We would expect to see these patterns in shell accumulation rates, community shifts as measured by percent abundance, and size changes within a species.

To explore how size information might be applied in this context, we reconsider the results of sediment studies of shell size variations in *O. universa*. Bé *et al.* [1973] assumed temperature controlled *O. universa* shell size and were able to correlate shell size from Indian Ocean core top sediments with SST as a paleo-SST proxy. Bé and Duplessy [1976] assumed this correlation applied through time and studied downcore shell size variations at two sites near the present-day Subtropical Convergence (STC): RC17-69, ≈500 km off the SE African coast (31.50°S 32.60°E) and RC9-150, ≈125 km off the SW Australian coast (31.28°S 114.5°E). They found *O. universa* shells were ≈200 μm larger during warm interglacial than colder glacial stages. They suggested that 450-μm sized shells track the location of the STC and concluded the STC moved as far north as 31°S (from its modern location of 38-40°S) during glacial stages.

Hutson [1980] disagreed. He concluded (1) the location of the STC was best described by a transition from a dominant subtropical to a subantarctic foraminiferal fauna and that the STC remained south of the location of RC17-69 during glacial stages and (2) size in *O. universa* was not diagnostic of the STC location. Hutson [1980] provided no explanation of what might be driving the observed glacial-interglacial size changes in *O. universa*.

Our results suggest an alternative interpretation for these size changes of *O. universa* in Indian Ocean sediments. Given the near-coastal environments of these two cores, the observed size differences are consistent with changes in ambient light of the waters in which *O. universa* grew. Smaller *O. universa* shells during glacial periods could imply either higher biomass (due to higher productivity) or cloudier conditions along the glacial Indian Ocean margin than today. Our study argues that productivity driven variations in water turbidity are more important than small changes in temperature as a control on the size of *O. universa* and other symbiotic species at midlatitude and high-latitude sites.

Conclusions

Temperature does not provide the sole or even dominant control on local foraminiferal size and distribution patterns in the California Current off southern Oregon. Temperature changes are uncorrelated with changes in standing stock or size of foraminiferal species in this study region except for *G. ruber*, which was near its thermal tolerance limit. Although temperature controls a foraminiferal species' distribution near the limits of its thermal tolerance, food and light appear to provide the primary control under more favorable temperatures.

Shallow-dwelling asymbiotic species (e.g., right-coiling *N. pachyderma*, *G. quinqueloba*, and *G. bulloides*), which survive by grazing, were most common off Oregon in high-

biomass waters with abundant food. These species exhibit a range of critical food thresholds below which each was absent. For example, *G. bulloides*, which has the greatest apparent food need of these species, is largely confined to the very high biomass upwelling waters within 100 km of the coast in the study area.

In contrast, ambient light levels seemed to determine the distribution of symbiont-bearing species, which increased in abundance as water turbidity decreased. Meager standing stocks and small shell sizes of symbiotic species such as *O. universa* and *N. dutertrei* are associated with high-biomass waters, while large individuals with greater standing stocks occur in low-biomass waters. These results suggest that the small individuals of symbiotic species preserved in sediments of high-biomass (high-turbidity) regions reflect stressed growth under light limitation and that larger specimens reflect less turbid waters and high symbiont activity. These field observations are consistent with laboratory studies of the foraminiferal host-symbiont complex.

This plankton tow study indicates mechanistic links between foraminiferal species composition and variations in light availability and food concentration driven by changes in oceanic productivity. Accordingly, these findings identify biological processes that support the reconstruction of oceanic productivity using multivariate transfer functions and foraminiferal faunal data [Mix, 1989a, b]. We suggest strategies for reconstructing paleoproductivity from shell size and the relative abundance of symbiotic and asymbiotic foraminifera. Future research on the reconstruction of oceanic paleotemperature and paleoproductivity should focus on developing strategies to determine when foraminiferal faunas are biologically (e.g., food and light) as opposed to thermally controlled.

Acknowledgments. We thank the captain and crew of R/V *Wecoma*, the Multitracers sediment trap group, and M. Hill and M. Willis for help with the MOCNESS. S. Richard helped process some of the MOCNESS samples as part of an REU summer project. C. Roesler provided 1991 PAR data for comparison to C_p . M. Abbott and T. Strub provided computer facilities for AVHRR analysis. J. Huyer and B. Smith gave helpful insights on hydrography. The text was improved by comments from N. Pisias, P. Wheeler, M. Abbott, L. Welling, and J. Watkins and insightful reviews from C. Ravelo and H. Spero. Funding for this project was provided by a NASA Graduate student fellowship to the first author and by NSF funding to the Multitracers project. Curation of the plankton tow samples at the NORCOR Marine Geological Repository at OSU was provided by a grant from the NSF.

References

- Bé, A. W. H., A method for rapid sorting of foraminifera from marine plankton samples, *J. Paleontol.*, **33**, 846-848, 1959a.
- Bé, A. W. H., Ecology of recent planktonic foraminifera; 1, Areal distribution in the western North Atlantic, *Micropaleontology*, **5**, 77-100, 1959b.
- Bé, A. W. H., Ecology of recent planktonic foraminifera, 2, Bathymetric and seasonal distributions in the Sargasso Sea off Bermuda, *Micropaleontology*, **6**, 373-392, 1960.
- Bé, A. W. H., An ecological, zoogeographic, and taxonomic review of recent planktonic foraminifera, in *Oceanic Micropaleontology*, vol. 1, edited by A. T. S. Ramsey, pp. 1-100, Academic, San Diego, Calif., 1977.
- Bé, A. W. H., and J. C. Duplessy, Subtropical convergence fluctuations and quaternary climates in the middle latitudes of the Indian Ocean, *Science*, **194**, 419-422, 1976.
- Bé, A. W. H., and W. H. Hamlin, Ecology of recent planktonic

- foraminifera. 3, Distribution in the North Atlantic during the summer of 1962, *Micropaleontology*, 13, 87-106, 1967.
- Bé, A. W. H., and W. H. Hutson, Ecology of planktonic foraminifera and biogeographic patterns of life and fossil assemblages in the Indian Ocean, *Micropaleontology*, 23, 369-414, 1977.
- Bé, A. W. H., and D. S. Tolderlund, Distribution and ecology of living planktonic foraminifera in the surface waters of the Atlantic and Indian Oceans, in *The Micropaleontology of Oceans*, edited by B. M. Funnel and W. R. Riedel, pp. 105-149, Cambridge Univ. Press, New York, 1971.
- Bé, A. W. H., S. M. Harrison, and L. Lott, *Orbulina universa* d'Orbigny in the Indian Ocean, *Micropaleontology*, 19, 150-192, 1973.
- Bé, A. W. H., C. Hemleben, O. R. Anderson, M. Spindler, J. Hacunda, and S. Tuntivate-Choy, Laboratory and field observations of living planktonic foraminifera, *Micropaleontology*, 23, 155-179, 1977.
- Bé, A. W. H., D. A. Caron, and O. R. Anderson, Effects of feeding frequency on life processes of the planktonic foraminifer *Globigerinoides sacculifer* in laboratory culture, *J. Mar. Biol. Assoc. U. K.*, 61, 257-277, 1981.
- Bé, A. W. H., H. J. Spero, and O. R. Anderson, Effects of symbiont elimination and reinfection on the life process of the planktonic foraminifer *Globigerinoides sacculifer*, *Mar. Biol. Berlin*, 70, 73-86, 1982.
- Bé, A. W. H., J. Bishop, M. Sverdløve, and W. Gardner, Standing stock, vertical distribution and flux of planktonic foraminifera in the Panama Basin, *Mar. Micropaleontol.*, 9, 307-333, 1985.
- Berger, W. H., Ecologic patterns of living planktonic foraminifera, *Deep Sea Res.*, 16, 1-24, 1969.
- Berger, W. H., Planktonic foraminifera: Sediment production in an oceanic front, *J. Foraminiferal Res.*, 1, 95-118, 1971.
- Bernhard, J. M., Postmortem vital staining in benthic foraminifera: Duration and importance in population and distributional studies, *J. Foraminiferal Res.*, 18, 143-146, 1988.
- Bijma, J., J. Erez, and C. Hemleben, Lunar and semi-lunar reproductive cycles in some spinose planktonic foraminifers, *J. Foraminiferal Res.*, 20, 117-127, 1990a.
- Bijma, J., W. W. Faber Jr., and C. Hemleben, Temperature and salinity limits for growth and survival of planktonic foraminifers in laboratory cultures, *J. Foraminiferal Res.*, 20, 128-148, 1990b.
- Bijma, J., H. Hemleben, H. Oberhänsli, and M. Spindler, The effects of increased water fertility on tropical spinose planktonic foraminifers in laboratory cultures, *J. Foraminiferal Res.*, 22, 242-256, 1992.
- Bradshaw, J., Ecology of living planktonic foraminifera in the north and equatorial Pacific Oceans, *Contrib. Cushman Found. Foraminiferal Res.*, 10, 25-64, 1959.
- Caron, D. A., and A. W. H. Bé, Predicted and observed feeding rates of the spinose planktonic foraminifer *Globigerinoides sacculifer*, *Bull. Mar. Sci.*, 35, 1-10, 1984.
- Caron, D. A., A. W. H. Bé, and O. R. Anderson, Effects of variations in light intensity on life processes of the planktonic foraminifer *Globigerinoides sacculifer* in laboratory culture, *J. Mar. Biol. Assoc. U. K.*, 62, 435-452, 1981.
- Caron, D. A., W. W. Faber Jr., and A. W. H. Bé, Effects of temperature and salinity on the growth and survival of the planktonic foraminifer *Globigerinoides sacculifer*, *J. Mar. Biol. Assoc. U. K.*, 67, 323-341, 1987.
- Climate: Long-Range Investigation, Prediction, and Mapping (CLIMAP) Project Members, The surface of the ice age Earth, *Science*, 191, 1131-1137, 1976.
- Cullen J. L., and W. L. Prell, Planktonic foraminifera of the northern Indian Ocean: Distribution and preservation in surface sediments, *Mar. Micropaleontol.*, 9, 1-52, 1984.
- Cullen J. J., M. R. Lewis, C. O. Davis, and R. T. Barber, Photosynthetic characteristics and estimated growth rates indicate grazing is the proximate control of primary production in the equatorial Pacific, *J. Geophys. Res.*, 97, 639-654, 1992.
- Curry, B., D. R. Ostermann, and M. V. S. Gupta, Foraminiferal production and monsoonal upwelling in the Arabian Sea: Evidence from sediment traps, in *Evolution of Upwelling Systems: Miocene to Present*, edited by C. P. Summerhayes, W. Prell, and K. C. Emeis, *Geol. Soc. Spec. Publ. London*, 64, 93-106, 1992.
- Dam, H. G., C. A. Miller, and S. H. Jonasdottir, The trophic role of mesozooplankton at 47°N, 20°W during the North Atlantic Bloom Experiment, *Deep Sea Res., Part II*, 40, 171-195, 1993.
- Dickson, M.-L. Nitrogen dynamics in a coastal upwelling regime, Ph.D. thesis, 214 pp., Oreg. State Univ., Corvallis, 1994.
- Dowset, H. J., The development of a long-range foraminiferal transfer function and application to the Pleistocene North Atlantic climatic extremes, *Paleoceanography*, 6, 259-273, 1991.
- Dryden, A. L., Accuracy in percentage representation of heavy mineral frequencies, *Proc. Natl. Acad. Sci. U.S.A.*, 17, 233-238, 1931.
- Dymond, J., E. Suess, and M. Lyle, Barium in deep-sea sediments: A geochemical proxy for paleoproductivity, *Paleoceanography*, 7, 163-183, 1992.
- Erez, J., A. Almogi-Labin, and S. Avraham, On the life history of planktonic foraminifera: Lunar reproduction cycle in *Globigerinoides sacculifer* (Brady), *Paleoceanography*, 6, 295-306, 1991.
- Faber, W. W., O. R. Anderson, J. L. Lindsey, and D. A. Caron, Algal-foraminiferal symbiosis in the planktonic foraminifer *Globigerinella aequilateralis*, I, Occurrence and stability of two mutually exclusive chrysophyte endosymbionts and their ultrastructure, *J. Foraminiferal Res.*, 18, 334-343, 1988.
- Faber, W. W., O. R. Anderson, and D. A. Caron, Algal-foraminiferal symbiosis in the planktonic foraminifer *Globigerinella aequilateralis*, II, Effect of two symbiont species on foraminiferal growth and longevity, *J. Foraminiferal Res.*, 19, 185-193, 1989.
- Fairbanks R., and P. Wiebe, Foraminiferal and chlorophyll maximum: Vertical distribution, seasonal succession, and paleoceanographic significance, *Science*, 209, 1524-1526, 1980.
- Fairbanks R. G., P. H. Wiebe, and A. W. H. Bé, Vertical distribution and isotopic composition of planktonic foraminifera in the western North Atlantic, *Science*, 207, 61-63, 1979.
- Fischer, K. M., Particle fluxes in the eastern tropical Pacific Ocean - Sources and processes, Ph.D. thesis, 225 pp., Oreg. State Univ., Corvallis, 1984.
- Ganssen, G., Isotopic analysis of foraminifera shells: interference from chemical treatment, *Palaeogeogr. Palaeoclimatol., Palaeoecol.*, 33, 271-276, 1981.
- Gardner, W. D., I. D. Walsh, and M. J. Richardson, Biophysical forcing of particle production and distribution during a spring bloom in the North Atlantic, *Deep Sea Res., Part II*, 40, 171-195, 1993.
- Hecht, A. D., An ecologic model for test size variation in recent planktonic foraminifera: Applications to the fossil record, *J. Foraminiferal Res.*, 6, 295-311, 1976.
- Hecht, A. D., and S. M. Savin, Phenotypic variation and oxygen isotope ratios in recent planktonic foraminifera, *J. Foraminiferal Res.*, 2, 55-57, 1972.
- Hemleben, C., M. Spindler, and O. R. Anderson, (Eds.), *Modern Planktonic Foraminifera*, 363 pp., Springer-Verlag, New York, 1988.
- Hofmann, E. E., K. S. Hedström, J. R. Moisan, D. B. Haidvogel, and D. L. Mackas, Use of simulated drifter tracks to investigate general transport patterns and residence times in the Coastal Transition Zone, *J. Geophys. Res.*, 96, 15,041-15,052, 1991.
- Hutson, W. H., The Agulhas Current during the Late Pleistocene: Analysis of modern faunal analogs, *Science*, 207, 64-66, 1980.
- Huyer, A., Coastal upwelling in the California Current System, *Prog. Oceanogr.*, 12, 1434-1450, 1983.
- Ikeda, M., and W. J. Emery, Satellite observations and modeling of meanders in the California Current System off Oregon and northern California, *J. Phys. Oceanogr.*, 14, 1434-1450, 1984.
- Imbrie, J. and N. G. Kipp, A new micropaleontological method for quantitative paleoclimatology: Application to a Late Pleistocene Caribbean core, in *The Late Cenozoic Glacial Ages*, edited by K. Turekian, pp. 71-181, Yale Univ. Press, New Haven, Conn., 1971.
- Jones, D. S., D. F. Williams, and H. J. Spero, More light on photosymbiosis in fossil mollusks: The case of *Mercenaria "tridacnoides"*, *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 64, 141-152, 1988.
- Jørgensen, B. B., J. Erez, N. P. Revsbech, and Y. Cohen, Symbiotic photosynthesis in a planktonic foraminiferan, *Globigerinoides sacculifer* (Brady), studied with microelectrodes, *Limnol. Oceanogr.*, 30, 1253-1267, 1985.
- Kipp, N. G., New transfer function for estimating past sea-surface conditions from sea-bed distributions of planktonic foraminiferal assemblages in the north Atlantic, in *Investigations of Late Quaternary Paleoclimatology and Paleontology*, edited by K. K. Turekian, *Geol. Soc. Am. Mem.* 145, 3-41, 1976.
- Klovan, J. E., and J. Imbrie, An algorithm and FORTRAN IV program

- for large scale Q-mode factor analysis, *J. Int. Assoc. Math. Geol.*, **3**, 61-77, 1971.
- Kroon D., and G. Ganssen, Northern Indian Ocean upwelling cells and the stable isotope composition of living planktonic foraminifera, *Deep Sea Res., Part A*, **36**, 1219-1236, 1989.
- Lauris, R. M., Coastal upwelling and the ecology of lower trophic levels, Ph.D. thesis, 121 pp., Oreg. State Univ., Corvallis, 1967.
- Longhurst, A. R., Vertical migration, in *The Ecology of the Seas*, edited by D. H. Cushing and J. J. Walsh, pp. 116-137, Saunders, Philadelphia, 1976.
- Loubere, P., Oceanographic parameters reflected in the seabed distribution of planktic foraminifera from the North Atlantic and Mediterranean Sea, *J. Foraminiferal Res.*, **11**, 137-158, 1981.
- Lyle, M., R. Zahn, F. Prahli, J. Dymond, R. Collier, N. Pisias, and E. Suess, Paleoproductivity and carbon burial across the California Current: The Multitracers transect, 42°N, *Paleoceanography*, **7**, 251-272, 1992.
- Mackas, D. L., L. Washburn, and S. L. Smith, Zooplankton community pattern associated with a California Current cold filament, *J. Geophys. Res.*, **96**, 14,781-14,798, 1991.
- Miles, G. A., Living planktonic foraminifera in the northeast Pacific Ocean, M.A. thesis, 131 pp., Univ. of Oreg., Univ. of Oreg. Press, Eugene, 1973.
- Mix, A. C., Pleistocene paleoproductivity: Evidence from organic carbon and foraminiferal species, in *Productivity of the Oceans: Past and Present*, edited by W. H. Berger, V. S. Smetacek, and G. Wefer, pp. 313-340, John Wiley, New York, 1989a.
- Mix, A. C., Influence of productivity variations on long-term atmospheric CO₂, *Nature*, **337**, 541-544, 1989b.
- Molfino, B., Statistics define ecologic controls of fossil planktonic forams (Abstract), in *ICP IV Abstract Volume, GEOMAR Rep. 15*, edited by M. Sarnthein, J. Thiede, and R. Zahn, p. 204, GEOMAR, Kiel, Germany, p. 204, 1992.
- Molfino, B., N. G. Kipp, and J. Morley, Comparison of foraminiferal, Coccolithophorid, and Radiolarial paleotemperature equations: Assemblage coherency and estimate concordancy, *Quat. Res.*, **17**, 279-313, 1982.
- Oberhänsli, H., C. Bénier, G. Meinecke, H. Schmidt, R. Schneider, and G. Wefer, Planktonic foraminifera as tracers of oceanic currents in the eastern south Atlantic, *Paleoceanography*, **7**, 607-632, 1992.
- Ortiz, J. D., Planktic foraminifera of the California Current: Last glacial maximum and present, Ph.D. thesis, 211 pp., Oreg. State Univ., Corvallis, 1995.
- Ortiz, J. D., and A. C. Mix, The spatial distribution and seasonal succession of planktonic foraminifera in the California Current off Oregon, September 1987-1988, in *Upwelling Systems: Evolution Since the Early Miocene*, edited by C. P. Summerhayes, W. L. Prell, and K. C. Emeis, *Geol. Soc. Spec. Publ. 64 London*, 197-213, 1992.
- Paduan, J. D., and P. P. Niiler, A lagrangian description of motion in northern California coastal transition filaments, *J. Geophys. Res.*, **95**, 18,095-18,109, 1990.
- Pak, H., D. A. Kiefer, and K. C. Kitchen, Meridional variations in the concentration of chlorophyll and microparticles in the North Pacific Ocean, *Deep Sea Res., Part A*, **35**, 1151-1171, 1988.
- Parker, F., Planktonic foraminiferal species in Pacific sediments, *Micropaleontology*, **8**, 219-254, 1962.
- Pond, S., and G. Pickard, *Introductory Dynamical Oceanography*, 2nd ed., 329 pp., Pergamon, Tarrytown, N.Y., 1983.
- Ravelo, A. C., R. G. Fairbanks, and S. G. H. Philander, Reconstructing tropical atlantic hydrography using planktonic foraminifera and an ocean model, *Paleoceanography*, **5**, 409-431, 1990.
- Sancetta, C., M. Lyle, L. Huesser, R. Zahn, and J. P. Bradbury, Late-Glacial to Holocene changes in the winds, upwelling and seasonal production of the northern California Current System, *Quat. Res.*, **38**, 359-370, 1992.
- Sautter, L., and R. Thunell, Seasonal succession of the planktonic foraminifera: Results from a four year time-series sediment trap experiment in the northern Pacific, *J. Foraminiferal Res.*, **19**, 253-267, 1989.
- Sautter, L., and R. Thunell, Planktonic foraminiferal response to upwelling and seasonal hydrographic conditions: Sediment trap results from San Pedro basin, southern California, *J. Foraminiferal Res.*, **21**, 347-363, 1991.
- Smith, A. B., Distribution of living planktonic foraminifera in the north-eastern Pacific, *Contrib. Cushman Found. Foraminiferal Res.*, **14**, 1-15, 1963.
- Smith, A. B., Living planktonic foraminifera collected along an east-west traverse in the north Pacific, *Contrib. Cushman Found. Foraminiferal Res.*, **15**, 131-134, 1964.
- Snedecor, G. W., and W. G. Cochran, *Statistical Methods*, 8th ed., 503 pp., Iowa State Univ. Press, Ames, 1989.
- Spero, H. J., Do planktic foraminifera accurately record shifts in the carbon isotopic composition of seawater ΣCO₂?, *Mar. Micropaleontol.*, **19**, 275-285, 1992.
- Spero, H. J., and S. L. Parker, Photosynthesis in the symbiotic planktonic foraminifer *Orbulina universa*, and its potential contribution to oceanic primary productivity, *J. Foraminiferal Res.*, **15**, 273-281, 1985.
- Spinrad, R. W., A calibration diagram of specific beam attenuation, *J. Geophys. Res.*, **91**, 7761-7764, 1986.
- Spinrad, R. W., H. Glover, B. B. Ward, L. A. Codispoti, and G. Kullenberg, Suspended particle and bacterial maxima in Peruvian coastal waters during a cold water anomaly, *Deep Sea Res., Part A*, **36**, 715-733, 1989.
- Stewart, R. H., *Methods of Satellite Oceanography*, 360 pp., Univ. of Calif. Press, Berkeley, 1985.
- Strub, P. T., P. M. Kosro, A. Huyer, and CTZ Collaborators, The nature of the cold filaments in the California Current System, *J. Geophys. Res.*, **96**, 14,743-14,768, 1991.
- Swenson, M. S., P. P. Niiler, K. H. Brink, and M. R. Abbott, Drifter observations of a cold filament off Point Arena, California, in July 1988, *J. Geophys. Res.*, **97**, 3593-3610, 1992.
- Thiede, J., and B. Jünger, Faunal and floral indicators of coastal upwelling, in *Upwelling Systems: Evolution Since the Early Miocene*, edited by C. P. Summerhayes, W. L. Prell, and K. C. Emeis, *Geol. Soc. Spec. Publ. London*, **64**, 47-76, 1992.
- Thunell, R., and L. R. Sautter, Planktonic foraminiferal faunal and stable isotopic indices of upwelling: A sediment trap study in the San Pedro Basin, Southern California Bight, in *Upwelling Systems: Evolution Since the Early Miocene*, edited by C. P. Summerhayes, W. L. Prell, and K. C. Emeis, *Geol. Soc. Spec. Publ. London*, **64**, 197-213, 1992.
- Walton, W. R., Techniques for recognition of living foraminifera, *Contrib. Cushman Found. Foraminiferal Res.*, **3**, 56-60, 1952.
- Watkins, J., A. C. Mix, and J. Wilson, Living planktonic foraminifera: Tracers of surface water masses and productivity regimes in the central Equatorial Pacific, *Deep Sea Res., Part II*, in press, 1995.
- Welling, L. A., N. G. Pisias, and A. K. Roelofs, Radiolaria as tracers of currents and water masses in the northern California Current System: A MOCNESS study, *Eos Trans. AGU*, **72(17)**, Spring Meet. Supplement, 156, 1991.
- Welling, L. A., N. G. Pisias, and A. K. Roelofs, Radiolarian microfauna in the northern California Current System: Indicators of multiple processes controlling productivity, in *Upwelling Systems: Evolution Since the Early Miocene*, edited by C. P. Summerhayes, W. L. Prell, and K. C. Emeis, *Geol. Soc. Spec. Publ. London*, **64**, 177-197, 1992.
- Wiebe, P. H., K. H. Burt, S. H. Boyd, and A. W. Morton, A multiple opening/closing net and environmental sensing system for sampling zooplankton, *J. Mar. Res.*, **34**, 313-326, 1976.
- Wiebe, P. H., A. W. Morton, A. M. Bradley, R. H. Backus, J. E. Craddock, V. Barber, T. J. Cowles, and G. R. Filerl, New developments in the MOCNESS, an apparatus for sampling zooplankton and micronekton, *Mar. Biol. Berlin*, **87**, 313-323, 1985.
- Zaneveld, J. R., R. W. Spinrad, and R. Bartz, Optical properties of turbidity standards, Ocean Optics VI, *Proc. SPIE Int. Soc. Opt. Eng.*, **208**, 159-168, 1979.

J. D. Ortiz, A. C. Mix, and R. W. Collier, College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis, OR 97331. (e-mail: jortiz@oce.orst.edu; amix@oce.orst.edu; rcollier@oce.orst.edu)

(Received September 19, 1994; revised July 5, 1995; accepted July 5, 1995.)