Variability in vertical distributions of planktonic foraminifera in the California Current: Relationships to vertical ocean structure

David B. Field

Scripps Institution of Oceanography, La Jolla, California, USA

[1]   Geochemical records from planktonic foraminifera are among the few means available to infer past changes in the upper ocean, although interpretations can be confounded by variability in foraminifera habitat depths. The principal environmental factors affecting foraminiferal vertical distributions were examined through 28 vertically stratified plankton tows taken off southern California in winter, spring, and summer. Each species has a dynamic range of preferred habitat depth, from the mixed layer to the thermocline, characterized by a unique relationship with environmental properties. *Globigerina bulloides*, *Neogloboquadrina pachyderma* (dextral), and *Neogloboquadrina dutertrei* can live near the surface but frequently live deeper as stratification increases and a particular isotherm deepens. *Globigerinoides ruber* and *Orbulina universa* vary more closely with the depth of the thermocline than the depth of a given isotherm. The shifts in habitat depth are of sufficient magnitude to affect $\delta^{18}O$ records. The effects of such shifts are observed for *G. bulloides* and *N. pachyderma* in Santa Barbara Basin sediments. Geochemical signatures from multiple species of foraminifera, each with a different predicted response to environmental change, can permit the detection of changes in habitat depth of a given species and thus more accurately indicate past changes in hydrographic structure.   *INDEX TERMS:* 3030 Marine Geology and Geophysics: Micropaleontology; 4267 Oceanography: General: Paleoceanography; 4855 Oceanography: Biological and Chemical: Plankton; 4870 Oceanography: Biological and Chemical: Stable isotopes; *KEYWORDS:* planktonic foraminifera, vertical variability

1. Introduction

[2]   While sea surface temperature (SST) represents the link between the ocean and atmosphere, determining the vertical structure of the upper ocean is critical for resolving the actual modes and mechanisms of climatic change. For example, decadal changes in the California Current System have largest temperature anomalies at the surface, due to changes in ocean-atmosphere heat flux [*Norton and McLain*, 1994; *Di Lorenzo et al.*, 2004]. In contrast, the largest anomalies associated with interannual El Niño warmings occur in the thermocline, in response to a deepening of isopycnals from changes in the basin-wide wind stress and propagation of coastally trapped waves [*Simpson*, 1992; *Norton and McLain*, 1994; *Miller*, 1996]. Different preferred habitat depths of planktonic foraminifera permit reconstruction of the vertical structure of the ocean by using the difference in a geochemical proxy for temperature ($\delta^{18}O$ or Mg/Ca) between near-surface and deeper-dwelling species [*Emiliani*, 1954; *Mulitza et al.*, 1997; *Patrick and Thunell*, 1997]. However, foraminifera may modify their habitat depths based on hydrographic conditions [*Fairbanks et al.*, 1982; *Sautter and Thunell*, 1991a]. Understanding vertical distribution patterns is therefore essential for reconstructing changes in hydrographic structure with geochemical records from different species of foraminifera.

[3]   Unique life-history traits result in different preferred habitat depths among species. Temperature, food, and light availability are the principal environmental factors known to affect the growth and distribution of planktonic foraminifera [*Fairbanks et al.*, 1982; *Caron et al.*, 1987; *Bijma et al.*, 1990]. The presence of spines is advantageous for prey capture and many spinose species have a more carnivorous diet [*Spindler et al.*, 1984]. The spinose species *Globigerina bulloides* is abundant in near-surface waters during times of high productivity and is generally representative of mixed layer temperatures [*Sautter and Thunell*, 1991a]. Other spinose species maintain symbionts (e.g., *Globigerinoides ruber*, *Orbulina universa*) and are more viable under higher light levels [*Caron et al.*, 1982; *Gastrich and Bartha*, 1988]. Symbiont bearing species occur more frequently in oligotrophic conditions and it is often assumed that light availability constrains them to the mixed layer. Many nonspinose species (e.g., *Neogloboquadrina pachyderma*, *Neogloboquadrina dutertrei*, *Globorotalia truncatulinoides*, *Globorotalia scitula*) are found within the thermocline and may have greater dietary preferences for phytoplankton, tintinnids or other ciliates, particulate organic carbon, or dead-sinking prey [*Spindler et al.*, 1984; *Hemleben et al.*, 1989].

[4]   The complexity in physical and biotic requirements results in considerable variability in the vertical distribution of a given species [*Sautter and Thunell*, 1991a]. As many hydrographic variables covary, it can be difficult to deter-
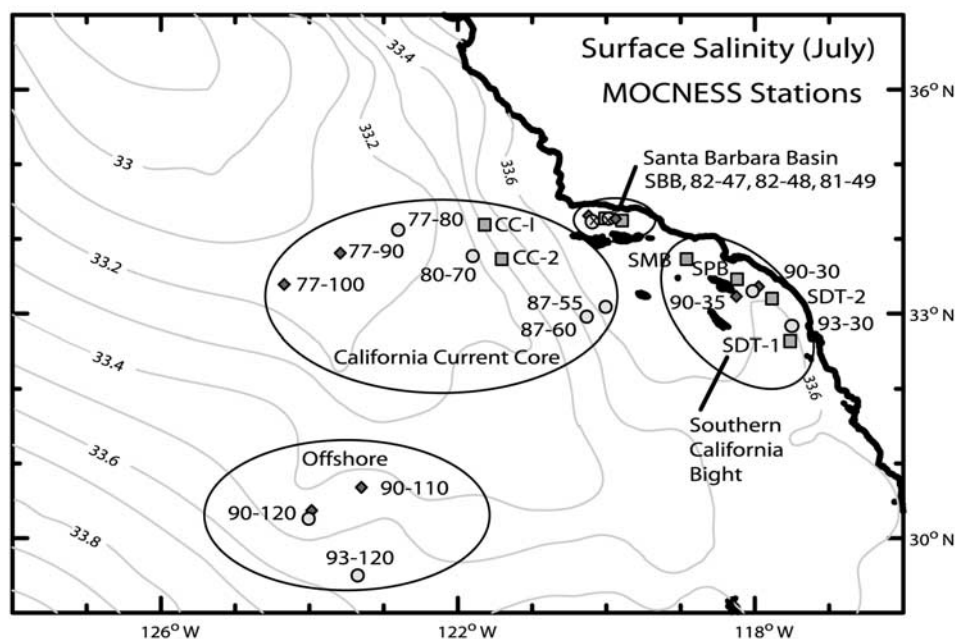
Figure 1. Location of MOCNESS sampling stations overlain on average surface salinity (July) as an indictor of circulation in the CCS [after *Lynn and Simpson*, 1978]. Station locations are shown for spring cruise SP 0103 (square), summer cruise NH 0107 (diamond), winter cruise NH 0001 (cross), and winter cruise JD 0201 (circle). The different hydrographic regions are circled (Santa Barbara Basin, California Current Core, Southern California Bight, and offshore). Sampling details in Table 1. See color version of this figure at back of this issue.

mine the causes of change in depth. Although many species are classified as "mixed layer dwellers" or "thermocline dwellers," some thermocline dwelling species (e.g., *N. pachyderma*, *N. dutertrei*) are found within the mixed layer during times of isopycnal shoaling and increased productivity [*Thunell and Reynolds*, 1984; *Sautter and Thunell*, 1991a]. Alternatively, species may modify their vertical distributions based on the depth of particular isotherms [*Sautter and Thunell*, 1991a], a preferred range of temperatures [*Fairbanks et al.*, 1982], chlorophyll [*Fairbanks and Wiebe*, 1980], or light [*Ortiz et al.*, 1995]. Such variability in habitat depths makes interpretation of sedimentary records challenging. For example, a diminished difference in $\delta^{18}O$ between a near-surface species and a deeper dwelling species could reflect an actual decrease in temperature gradient, a change in depth of either species, or both.

[5] Downcore environmental signals from foraminifera primarily reflect changes in the temperature and/or geochemical composition of a species' preferred habitat. However, acquired signatures can be confounded with changes in the timing or depth of preferred habitat or through indirect processes. There can be offsets in isotopic ratios due to species-specific intrinsic processes [*Shackleton et al.*, 1973], symbiotic algae [*Spero*, 1992], and dissolution [*Berger and Killingley*, 1977]. These indirect processes contribute less to downcore variability if test size and type are kept constant. However, changes in preferred habitat depth are particularly problematic because temperature gradients in the upper ocean can be greater than temperature variations occurring through time at a given depth.

[6] This study describes the vertical distributions of planktonic foraminifera in the California Current System (CCS). The CCS off southern California is the site of this study for several reasons: a wide range of hydrographic conditions in space and time, proximity to the Santa Barbara Basin (SBB) and other nearby basins that contain valuable archives of climatic changes, and the availability of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program to provide a historical perspective and sampling opportunity. The large number of stations sampled (28) with fine vertical sampling resolution taken across locations where many environmental variables are decoupled from one another make this one of the most detailed studies of foraminiferal vertical distributions to date. Observations of foraminiferal distributions in different hydrographic conditions of the CCS may be analogous to variations in climate state at a single location and thus help distinguish different mechanisms of change. I characterize species-specific changes in habitat depths in response to environmental conditions and show how such changes can affect geochemical signatures.

2. Methods

2.1. Vertical Sampling

[7] A total of 28 MOCNESS (Multiple Opening-Closing Net and Environmental Sensing System) [*Wiebe et al.*, 1985] collections of vertically stratified plankton samples were taken off southern California from the winter, spring, and summer seasons (Figure 1; Table 1). Summer and winter

Table 1. Stations Sampled With a MOCNESS[a]

Cruise	Station	Date	Time, PST (Begin Tow)	Latitude	Longitude	Day/Night
NH 0001	nh82-47-1	1/19/2000	19:13	34.28	119.96	night
NH 0001	nh82-47-2	1/19/2000	23:43	34.28	119.96	night
SP 0103	SP-CC1	3/7/2001	8:25	34.19	121.64	day
SP 0103	SP-CC2	3/7/2001	17:58	33.73	121.41	dusk
SP 0103	SP-SBB1	3/15/2001	0:49	34.28	119.81	**night**
SP 0103	SP-SBB2	3/15/2001	8:44	34.35	120.00	**day**
SP 0103	SP-SMB	3/15/2001	21:15	33.73	118.92	**night**
SP 0103	SP-SPB	3/16/2001	7:46	33.46	118.24	**day**
SP 0103	SP-SDT 1	3/8/2001	0:55	32.64	117.53	night
SP 0103	SP-SDT2	3/16/2001	17:05	33.20	117.77	dusk
NH 0107	NH90-120	7/13/2001	21:09	30.37	123.97	dusk
NH 0107	NH90-110	7/14/2001	7:07	30.68	123.30	day
NH 0107	NH90-35	7/16/2001	15:09	33.23	118.25	**day**
NH 0107	NH90-30	7/16/2001	22:00	33.36	117.95	**night**
NH 0107	NH82-47	7/22/2001	13:08	34.28	119.93	day
NH 0107	NH82-48	7/22/2001	19:10	34.31	120.24	dusk
NH 0107	NH77-100	7/24/2001	16:16	33.39	124.34	**day**
NH 0107	NH77-90	7/25/2001	2:31	33.73	123.68	**night**
JD 0201	JD93-120	1/27/2002	12:52	29.50	123.35	**day**
JD 0201	JD90-120	1/27/2002	19:36	30.26	124.01	**night**
JD 0201	JD87-55	1/31/2002	20:52	33.09	120.01	night
JD 0201	JD87-60	2/1/2002	3:32	32.98	120.18	night
JD 0201	JD82-47	2/5/2002	14:48	34.27	119.97	**day**
JD 0201	JD81-49	2/6/2002	0:08	34.23	120.19	**night**
JD 0201	JD80-70	2/6/2002	16:44	33.77	121.80	dusk
JD 0201	JD77-80	2/8/2002	12:40	34.03	122.57	day
JD 0201	JD90-30	2/10/2002	15:24	33.30	118.03	**day**
JD 0201	JD93-30	2/11/2002	3:57	32.85	117.32	**night**

[a]Paired stations that sampled the same hydrographic region are in adjacent rows. Paired stations used for day/night comparisons are shown in bold.

sampling was done on the quarterly CalCOFI surveys at standard CalCOFI stations on the R/V *New Horizon* (NH 0107 and NH 0001) and the R/V *David Star Jordan* (JD 0201). Eight stations were sampled around the Southern California Bight on the R/V *Sproul* in March 2001 on cruise SP 0103 (Table 1).

[8] MOCNESS collections (1 m^2 mouth opening, 120 μm mesh) generally consisted of nine depth strata. Targeted depth intervals were usually 0–12, 12–25, 25–38, 38–50, 50–65, 65–80, 80–100, 100–175, and 175–250 m, and targeted sample volumes were 250 m^3 or more. At some stations, where the thermocline was deep, the 100–175 m interval was divided into two intervals while two intervals in the upper mixed layer were combined (JD93-120, JD90-120; NH90-120 NH77-90; SP-CC2). On several occasions a net did not drop or two nets dropped at once, thus some depth strata were not sampled or two depth strata were combined into one. The first net change did not register mechanically at NH90-120, NH90-30, and NH82-47 and thus the bottom interval was not sampled.

[9] Sampling locations were chosen to represent end-members of different vertical profiles of temperature and chlorophyll *a* (e.g., hydrography) across the seasonal cycle in the California Current System (CCS). Although no samples were taken in fall, hydrographic conditions of the fall season generally lie between end-members of other seasons. Two stations were sampled within each hydrographic condition to assess reproducibility of vertical distribution patterns. When possible, sampling within a hydrographic region was done during both daytime and nighttime to test for diel migration. The different water masses and circulation patterns of the CCS that cause the

wide variations in hydrographic structure are briefly summarized here following *Lynn and Simpson* [1978].

2.2. Oceanographic Setting: The California Current System

[10] High atmospheric pressure offshore of the CCS forces equatorward winds and the associated flow of the California Current (CC) while expansion of the Aleutian Low results in weakened flow and a deepening of isopycnals. The meandering equatorward flow is characterized by cool temperatures and a low salinity core (Figure 1). The CC overlies colder, saltier, nutrient rich waters. Shoaling of isopycnals brings the underlying waters to the surface, resulting in greater productivity and a reduced mixed layer depth [*Hayward and Venrick*, 1998]. Isopycnal movements are caused by coastal upwelling, geostrophic flow of the CC, and changes to the basin-wide wind stress [*Roemmich*, 1989; *Brink and Cowles*, 1991; *Miller*, 1996]. Isopycnals (isohalines) are shallowest near the coast due to the combined influence of upwelling events year-round and the flow of the CC offshore (Figure 1). Waters over the SBB are in an area of strong isopycnal shoaling but are affected by waters from the core of the CC and the Southern California Bight [*Hendershott and Winant*, 1996].

[11] A cyclonic eddy within the Southern California Bight results in SSTs similar to the region offshore of the CC core, but with shallower mixed layer depths and greater productivity [*Lynn and Simpson*, 1978]. Upwelling can occur within the Bight in spring. Offshore of the CC, waters become more typical of the North Pacific subtropical gyre. This region is characterized by a deeper permanent thermo-

cline, lower productivity, deeper chlorophyll maximum, and higher temperatures.

2.3. Hydrographic Analyses

[12] The pycnocline depth was defined as the shallowest depth at which N^2 (buoyancy frequency) values reach >75% of the maximum N^2 value. N^2 values reflect changes in the density gradient and the potential for vertical mixing. N^2 values were approximated by:

$$N^2 = \frac{gd\rho}{\rho dz}$$

where g = gravitational acceleration, ρ = seawater density, and z = depth [*Pond and Pickard*, 1991]. One meter averages of density were obtained from the upcast of the MOCNESS profile. Since changes in density are primarily controlled by changes in temperature in this region (except at JD77-80), N^2 values indicate changes in the temperature gradient. While foraminiferal distributions were compared to the pycnocline depth, the discussion will refer to the thermocline rather than the pycnocline. Foraminiferal distributions were also compared to the depth of the 11.5°C isotherm, 33.6 isohaline, and 25.5 isopycnal, as these isopleths were present at all stations.

[13] Profiles of chlorophyll *a* were determined from each cruise-wide relationship between extracted chlorophyll *a* values measured from water bottle samples and in vivo fluorescence as measured from the CTD cast at the CalCOFI stations (NH 0001, NH 0107, JD 0201) or the MOCNESS in vivo fluorometer (SP 0103). The light shield was not used since it may interfere with flow over the fluorometer on a MOCNESS frame. Consequently, near-surface fluorescence values of daytime casts from cruise SP 0103 were subjected to red light contamination of the fluorometer's sensor. Examination of the raw data showed that the light contamination occurred in the upper 13 m (SP-CC1) and upper 10 m (SP-SBB2). Values of chlorophyll for the upper mixed layer were extrapolated from averaged values of the uncontaminated portion of the mixed layer. At SP-SPB the downcast profile was used since deployment was at dawn, before significant daylight could contaminate the signal.

2.4. Foraminifera Enumerations

[14] Samples were preserved in 95% ethyl alcohol buffered with tris (hydroxymethyl) aminomethane. The alcohol was changed after 24 hours. Each MOCNESS sample was divided with a Folsom splitter. One split was ashed using the high temperature combustion technique [*Sachs et al.*, 1964]. For cleaning, samples were then heated at approximately 100°C in a 15% solution of hydrogen peroxide buffered with sodium pyrophosphate. Dried samples were sieved into five different size fractions (120–150, 150–180, 180–212, 212–300, and >300 μm). Counts were made from each size fraction, or a split of the size fraction such that more than 200 tests were counted in each size fraction. Although foraminifera species can be complexes of several genotypes [*Darling et al.*, 2000], there are presently no corresponding morphological classifications. Species iden-

tification followed the taxonomy of *Hemleben et al.* [1989] with PD-intergrade (*N. pachyderma* – *N. dutertrei* intergrade) distinctions made following *Peeters et al.* [1999].

[15] On several occasions a MOCNESS net tore, rendering the depth stratum counts nonquantitative. This occurred at stations NH90-110 (43–59 m), NH77-90 (48–64 m), JD82-47 (49–63 m), JD93-120 (46–61 m), SP-CC2 (21–33 m), and SP-SDT-1 (23–34 m). For each of these strata except one, the density of each species was interpolated by averaging the densities from neighboring depth strata. Comparison of the interpolated densities with values from paired stations indicate that there are no peaks in the paired profile that occur within the interpolated interval, except for *G. bulloides* from 48–63 m at NH77-100. Thus densities of *G. bulloides* from the stratum at NH77-100 were used for the stratum at NH77-90. At each station for which a bottom stratum was not sampled, densities at the deepest stratum of the paired station were low, represented a small portion of the population, and were thus substituted for the missing stratum to keep analyses consistent.

[16] Several samples from collections over the SBB indicate problems of dissolution. Samples from 13–25, 25–37, and 37–49 m from NH82-47 and the sample from 11–23 m from NH82-48 contained very large amounts of phytoplankton. Vertically integrated tows from 200–0 m from the same station contained very few foraminifera (but large amounts of algae), which is in contrast to the higher abundances of foraminifera found beneath the chlorophyll maximum in stratified MOCNESS samples. The algae lowered the sample pH and may have caused dissolution within the vertical sample and the samples within the chlorophyll maximum. However, very high levels of chlorophyll *a* may have a negative effect on foraminifera abundances in the ocean [*Oberhänsli et al.*, 1992] and could also explain the absence of foraminifera in the stratified samples. The surface strata at NH82-47 and NH82-48 contained no algae and showed no evidence of dissolution. At JD81-49 there was considerable algae in the 11–23 m stratum and an absence of foraminifera, thus densities were interpolated from neighboring strata.

2.5. Defining Central Tendencies

[17] Depth intervals containing select percentiles of the total number of integrated foraminifera in the water column (sum of #/m^3 in each stratum times stratum breadth) were calculated to best characterize vertical distributions of a species. The core 25%, 50%, and 75% intervals are defined as the depth limits that contain the desired percentage of tests in the water column by minimizing the vertical distance between the depth limits. For example, the summation for a typical profile will begin at the sampling stratum with highest foraminiferal densities and move 1 m at a time through the strata above or below, whichever has the next highest densities, until each desired percentile is reached. Minimizing the vertical range ensures that the depth range spans the averaged maximum densities of the population (the preferred habitat) and should be less susceptible to biases from empty or sinking tests. The core 25% (50% and 75%) intervals were calculated for each species for which >25 (>15) tests were counted in a vertical profile.

However, an overriding criterion for the depth limit solutions was that the 50% (75%) depth interval solution must span the 25% (50%) depth interval. The midpoint of the core 25% interval is considered to be the median depth of the population while the intervals themselves indicate the dispersion of the population.

3. Results

3.1. Hydrographic Structure and Foraminiferal Distributions

[18] Species distributions across the different environmental characteristics of the CCS off southern California are grouped by region and shown in Figures 2, 3, 4, and 5. Species shown are chosen based on their abundance and relevance to sedimentary studies. Other species are shown in an electronic supplement.[1] Tables of the integrated abundance and percent composition of each species at each station are also available in an electronic supplement. Distributions and abundances of species between paired stations are generally similar but become increasingly different with changes in hydrographic structure. For example, compare and contrast paired stations SP-SBB1 and SP-SBB2 (Figure 2), SP-CC1 and SP-CC2 (Figure 3), NH90-30 and NH90-35 (Figure 4), and the offshore stations (Figure 5).

[19] The shallow thermocline over the SBB resulted in relatively high abundances of several species, particularly *G. bulloides* (Figure 2). *N. pachyderma* (dextral; hereafter referred to as *N. pachyderma*) was quite abundant in winter and *G. quinqueloba* was quite abundant in spring (see supplements). There was a clear subsurface chlorophyll maximum and gradual change in temperature in the upper 50 m at most of the winter stations (nh82-47-1, nh82-47-2, JD81-49) which made definition of a pycnocline depth ambiguous. Vertical distributions of species in the SBB were generally less distinguished from one another across seasons than other regions.

[20] Varying vertical distributions in the CC core (Figure 3) reflect its complex circulation. Stations along the inshore side of the CC core had well-developed mixed layers and higher overall abundances, particularly of *N. pachyderma*, primarily within the mixed layer. The spring stations (CC1 and CC2) had lower salinities, typical of CC core waters, while the winter stations (JD87-55 and JD87-60) had higher salinities, typical of the most inshore edge of the CC core (see Figure 1). The four stations in the outer core of the CC had lower overall abundances, lower salinities and complex thermocline features, typical of the lower productivity of the outer core of the CC.

[21] Many profiles within the Southern California Bight (Figure 4) had relatively stratified conditions, subsurface chlorophyll maxima, and moderate abundances of *G. bulloides*, *G. ruber*, *N. pachyderma*, *N. dutertrei*, and other species. The exceptions occurred during the spring cruise where profiles at SP-SMB, SP-SPB, and SP-SDT2 were more similar to upwelling conditions

and the abundances and distributions of species were more similar to SBB stations. Station SP-SDT1 was sampled eight days earlier than SP-SDT2 (during the spring transition to upwelling conditions) and to the south (Figure 1). The two stations had very different chlorophyll profiles, species compositions and vertical distributions (Figure 4). During summer (NH90-30 and NH90-35), there was a strong decoupling between the depth of the thermocline (16 and 19 m) and the depth of the chlorophyll maximum (45 and 45 m). There were subsurface maxima in the abundance of all species in summer, including *G. ruber* and *G. bulloides*.

[22] SST in the offshore region was similar to the Bight during summer and winter but the thermocline was considerably deeper and species assemblages offshore were dramatically different than other regions (Figure 5). *G. ruber* dominated the summer assemblage. *G. ruber*, *O. universa*, *G. truncatulinoides*, and other species made up much of the winter assemblage (Figure 5; also see supplement). *G. bulloides* and *N. pachyderma* were scarcely present in either season. Both foraminifera and chlorophyll *a* had broad vertical distributions offshore.

3.2. Test Sizes

[23] Test size can indicate viability and stages of growth. All species examined show an increase in median size with depth across all stations, although the patterns and magnitude of size changes differ by species (Figure 6). The increase in size is significant based on the Spearman's rank correlation for *G. bulloides* ($r^2 = 0.94$, $p < 0.0001$), *N. pachyderma* ($r^2 = 0.69$, $p < 0.01$), *N. dutertrei* ($r^2 = 0.80$, $p < 0.01$), and the PD-intergrade ($r^2 = 0.77$, $p < 0.01$). *G. bulloides* (*N. dutertrei*) shows greater differences in size with depth than *N. pachyderma* (PD-intergrade, *G. ruber*, *G. scitula*) in the stations shown in Figure 6 (as well as stations and species not shown). Profiles chosen for Figure 6 are those where foraminiferal densities are high and vertical distributions differ. Average sizes are shown for strata where >35 individuals were counted in all size fractions.

[24] Larger test sizes are generally associated with lower densities in deeper strata, with several exceptions. At station JD93-30 a significant proportion of the total number of tests of both *G. bulloides* and *N. pachyderma* are found below 100 m (Figure 6). Stations JD90-30 and SP-SDT1 show similar patterns. Most individuals of *G. bulloides* and *N. pachyderma* in the nonashed split of the sample from 174–100 m at JD93-30 contain protoplasm and DNA was extracted and amplified from *G. bulloides* (C. de Vargas, personal communication, 2003), indicating that individuals were alive at the time of collection. Average test size of *N. dutertrei* often increases in deeper strata where densities remain high. Largest test sizes of *N. dutertrei* in all strata were observed in the Southern California Bight stations in summer (NH90-30 and NH90-35). Larger test sizes of *G. ruber* in deeper strata are only associated with high densities at JD93-120.

[25] A *t* test shows that the average test sizes of the PD-intergrade (164 μm) are not significantly larger than *N. pachyderma* (162 μm; $t = 1.85$, N = 230; $p = 0.08$).

---

[1]Auxiliary material is available at ftp://ftp.agu.org/apend/pa/2003PA000970.
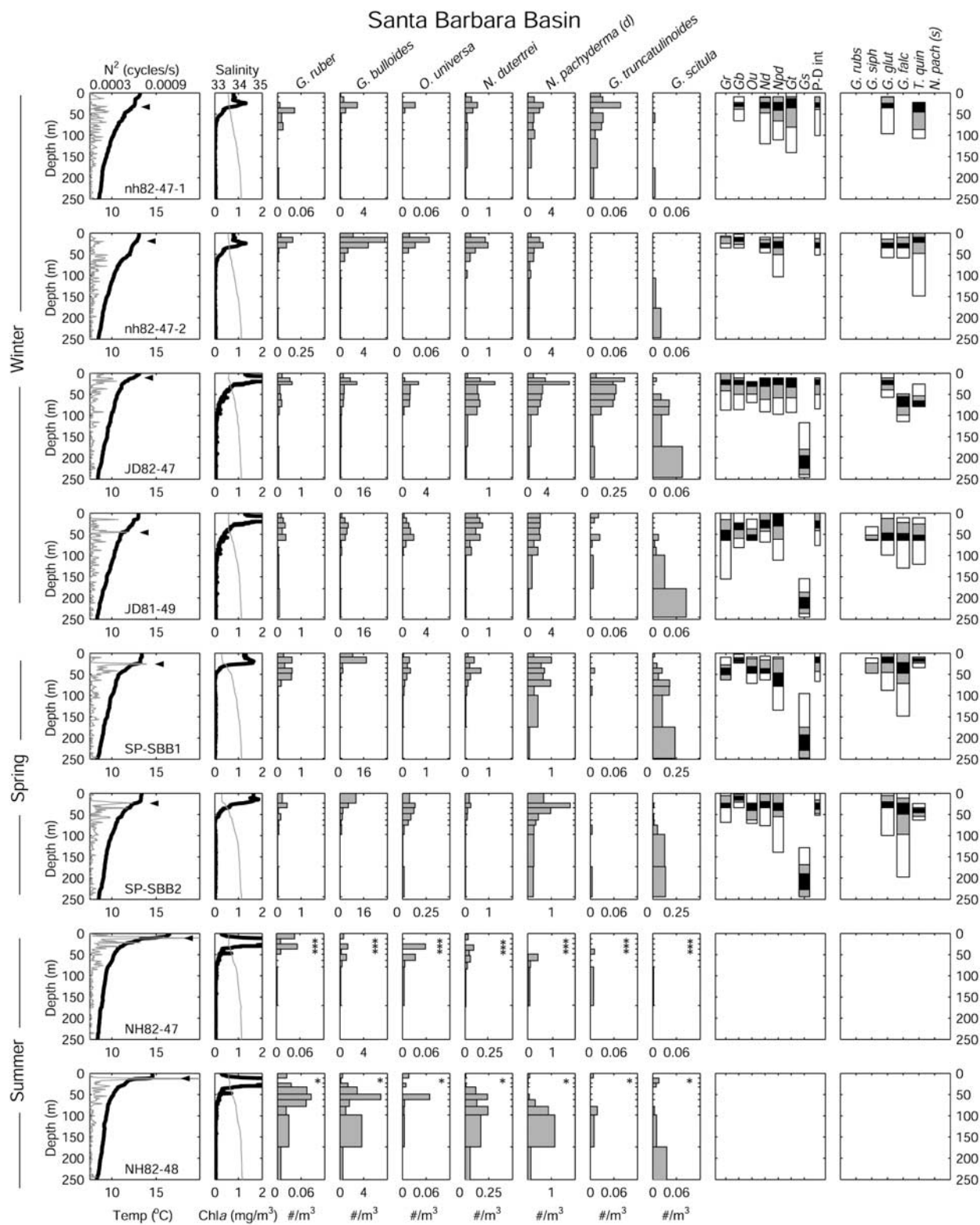
Figure 2

However, both of these means are smaller than *N. dutertrei* (185 μm; $t = 10.5$, $N = 221$; $p < 0.0001$; $t = 11.2$, $N = 221$; $p < 0.0001$).

3.3. Diel Vertical Migration

[26] Patterns of vertical distribution determined by hydrography could be confounded by diel vertical migrations. There were seven hydrographic conditions sampled that provided a basis for testing for diel vertical migration (see Table 1). Species with symbiotic algae [*Hemleben et al.*, 1989] had median distributions 16 m shallower in the day than night (Figure 7a; $t = 3.92$; $p < 0.005$). A portion of this difference may stem from the unintended result that the average depth of the pycnocline from the day stations was 10 m shallower than the night stations. Since the habitat depths of *G. ruber* and *O. universa* vary with the depth of the pycnocline (see below), the 10 m pycnocline offset could cause an offset in habitat depth of similar magnitude. Comparing the difference in the vertical distance of the median of the symbiont bearing species to the depth of the pycnocline (rather than the surface) still resulted in daytime depths 6 m shallower ($t = 1.94$; $p < 0.05$).

[27] In contrast, the average day-night difference was 10 m in both nonsymbiont and facultative symbiont-bearing species [*Hemleben et al.*, 1989] and was not significant (Figure 7b; $t = 1.00$; $p = 0.32$). The offset of these species was similar to the offset in pycnocline depth between the same stations. Diel vertical migrations, where present, were of limited amplitude and unlikely to be primary determinants of vertical distributions.

3.4. Effects of Environmental Properties on Foraminiferal Distributions

[28] Distinguishing between the effects of environmental variables on foraminiferal distributions is possible for properties that were weakly or moderately correlated with one another. Many, but not all, of the important environmental variables were decoupled in this study (Table 2). The depth of the 11.5°C isotherm was chosen to be representative of the depths of the 33.6 isohaline and the 25.5 isopycnal due to strong covariations between these isopleths and the chlorophyll maximum. Since stratification (temperature difference between 0 and 150 m) is predominantly controlled by SST (Table 2), only SST was chosen for comparison to vertical distributions.

[29] The three species that had the most variance in vertical distribution explained by the depth of the pycnocline (Figure 8) have symbiotic algae (*G. ruber* and *O. universa*) or are facultative symbiont-bearing (*G. glutinata*), although the variance explained is modest. Note that the symbols in Figures 8–10 represent different levels of integrated abundances. *G. ruber* generally occurred in the mixed layer, but was usually most abundant at the base of the mixed layer (Figure 8a) where chlorophyll concentrations were higher and light levels lower than just below the surface. There were four times when the integrated abundances of *G. ruber* were above average and a significant portion (or all) of its core 25% was found within the pycnocline (Figure 8a). Although *O. universa* can be abundant within the mixed layer, it was generally centered around the pycnocline (Figure 8b). Both species showed similar changes in depth with changes in the depth of the pycnocline and the 11.5°C isotherm (Table 3). The more variable depth distributions of *G. glutinata* (Figure 8c) may result from their reduced abundances and considerably lower number of tests counted (see supplement).

[30] Changes in habitat depth of *G. bulloides* were best explained by the depth of the chlorophyll maximum and the 11.5°C isotherm, but not by the depth of the pycnocline (Figure 9; Table 3). Although highest abundances of *G. bulloides* frequently occurred within the mixed layer, high abundances often spanned the pycnocline or occurred beneath the pycnocline. At all winter stations over the SBB there was some thermal stratification within the upper 20 m, which resulted in a subsurface peak in chlorophyll within the shallow thermal gradient. Abundances of *G. bulloides* were particularly high at JD82-47, but moderately high and subsurface at all winter stations (Figure 2). Several of these stations (nh82-47-1, JD81-49) had temperature gradients in the near-surface that did not meet the 75% maximum N^2 value criteria but temperatures ranged from 0.5–1.0°C less than SST at depths of maximum abundance (Figure 2). Samples spanning the chlorophyll maximum from the summer stations over the SBB may have experienced dissolution. However, the sample from the mixed layer stratum had no algae or dissolution but low abundances of *G. bulloides* relative to deeper strata, confirming that a greater portion of the population was found beneath the mixed layer at this time (Figure 2). Wintertime tows from the Southern

Figure 2. Vertical distributions of hydrographic properties and planktonic foraminifera over the Santa Barbara Basin. Paired stations are in adjacent rows. Temperature (thick line) and N^2 (thin line) are in the first graph in each row, together with the cruise and station designation. Triangles indicate calculated pycnocline depth from vertical profiles of N^2. The second graph in each row illustrates chlorophyll *a* (thick line) and salinity (thin line). Next are vertical distributions for the seven principal species of this study. Five different scaling factors, incremented by factors of four, are used to facilitate comparisons of abundance. Second panel from the right illustrates the core 25, 50, and 75% intervals of each of these species marked by black, gray, and white shading, respectively (*G. rubber*, Gr; *G. bulloides*, Gb; *O. universa*, Ou; *N. dutertrei*, Nd; *N. pachyderma* (dex.), Npd; *G. truncatulinoides*, Gt; *G. scitula*, Gs; and PD-int, PD-intergrade). The final graph in each row indicates summary vertical distributions of other species: *Globoturborotalita rubescens* (*G. rubs*), *Globigerinella siphonifera* (*G. siph*), *Globigerinita glutinata* (*G. glut*), *Globigerina falconensis* (*G. falc*), *Turborotalita quinqueloba* (*T. quin*), and *N. pachyderma* (sinistral; *N. pach* (s)). Potential dissolution in several samples of the summer stations prevented calculations of core intervals and are marked by asterisks.
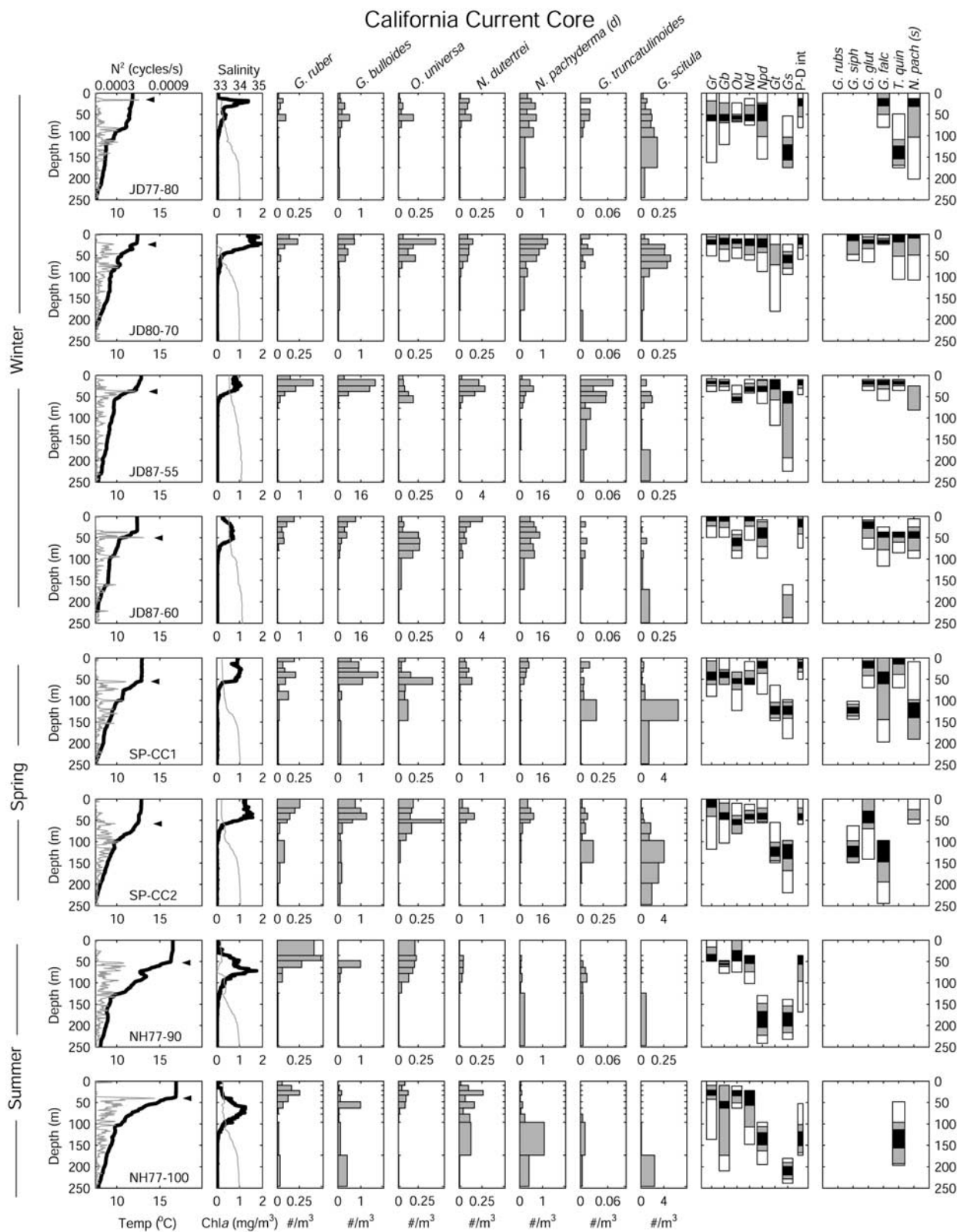
Figure 3. Vertical distributions of hydrographic properties and planktonic foraminifera in the California Current core. Details as in Figure 2.
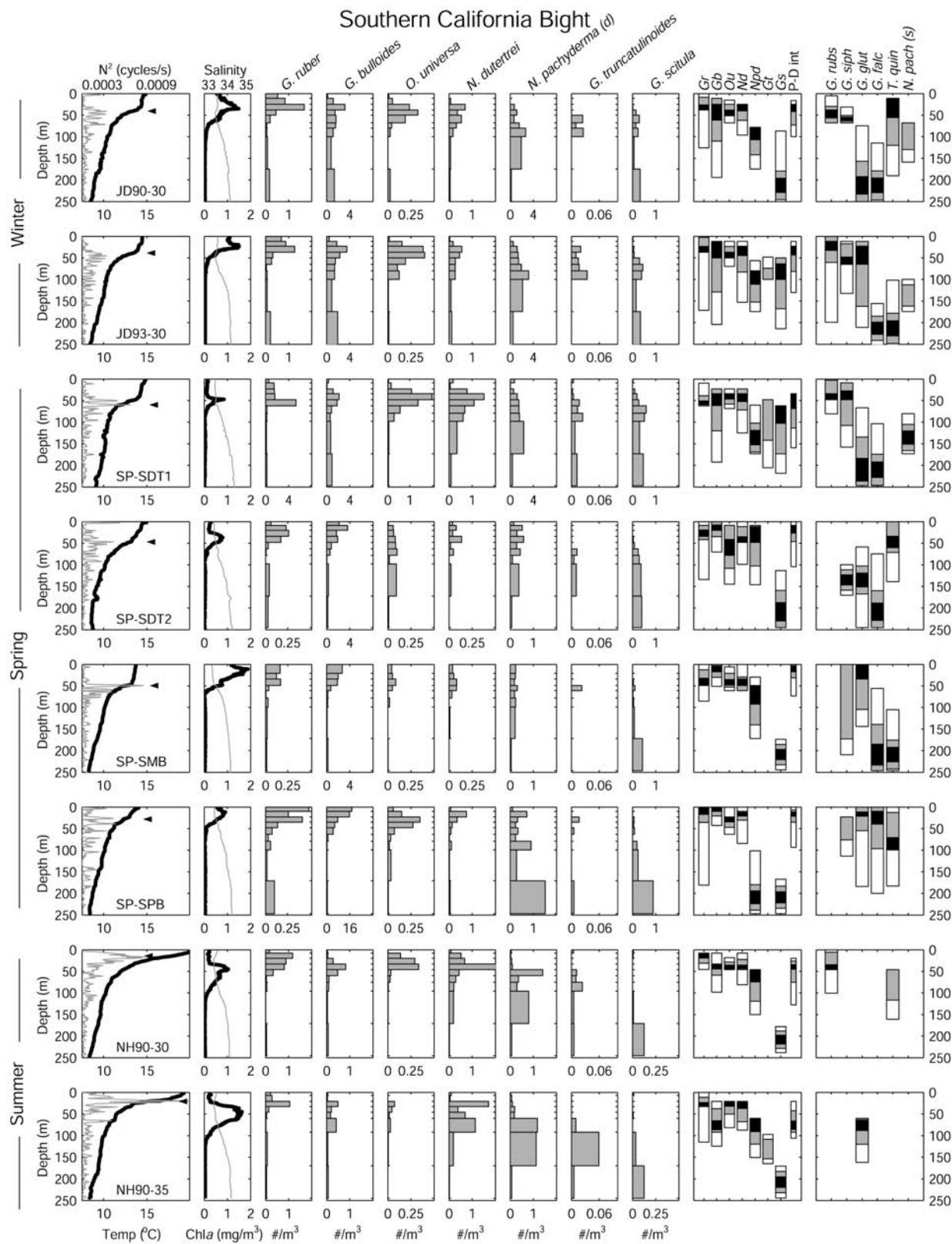
Figure 4. Vertical distributions of hydrographic properties and planktonic foraminifera in the Southern California Bight. Details as in Figure 2.
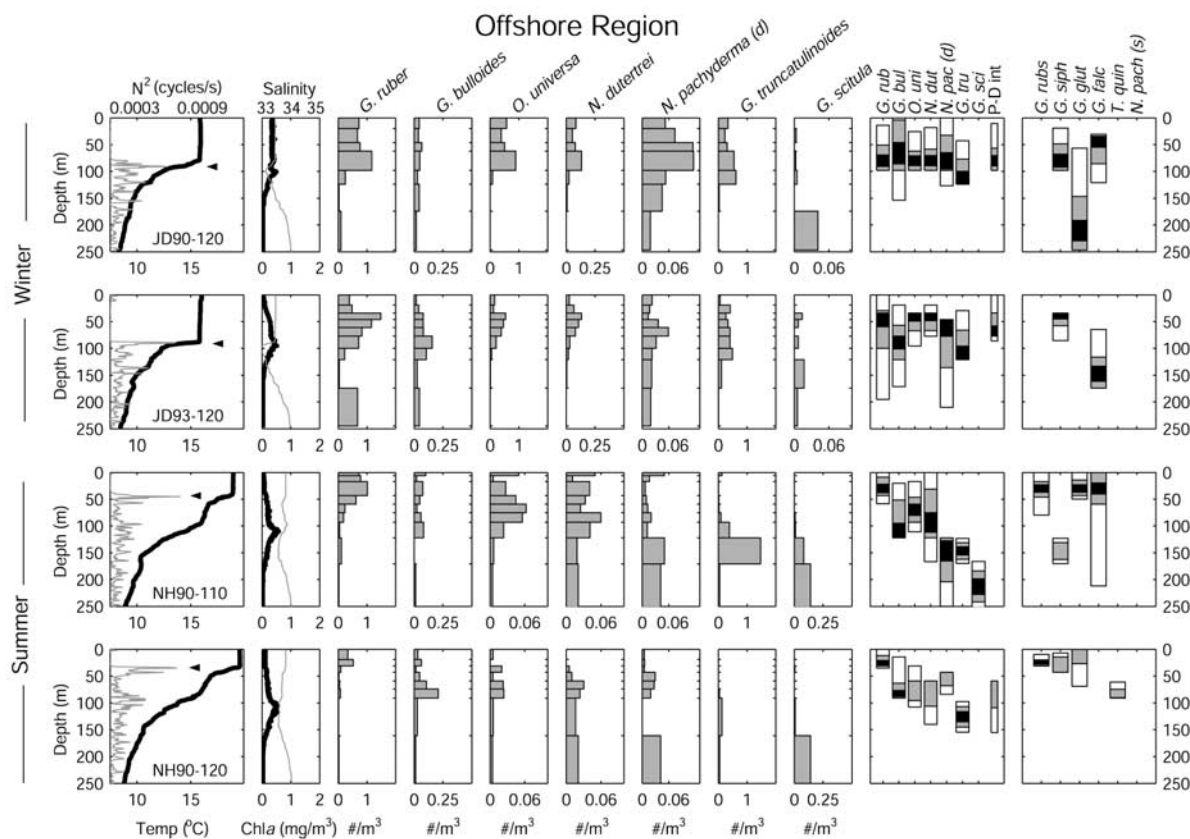
Figure 5. Vertical distributions of hydrographic properties and planktonic foraminifera in the region offshore of the California Current core. Details as in Figure 2.
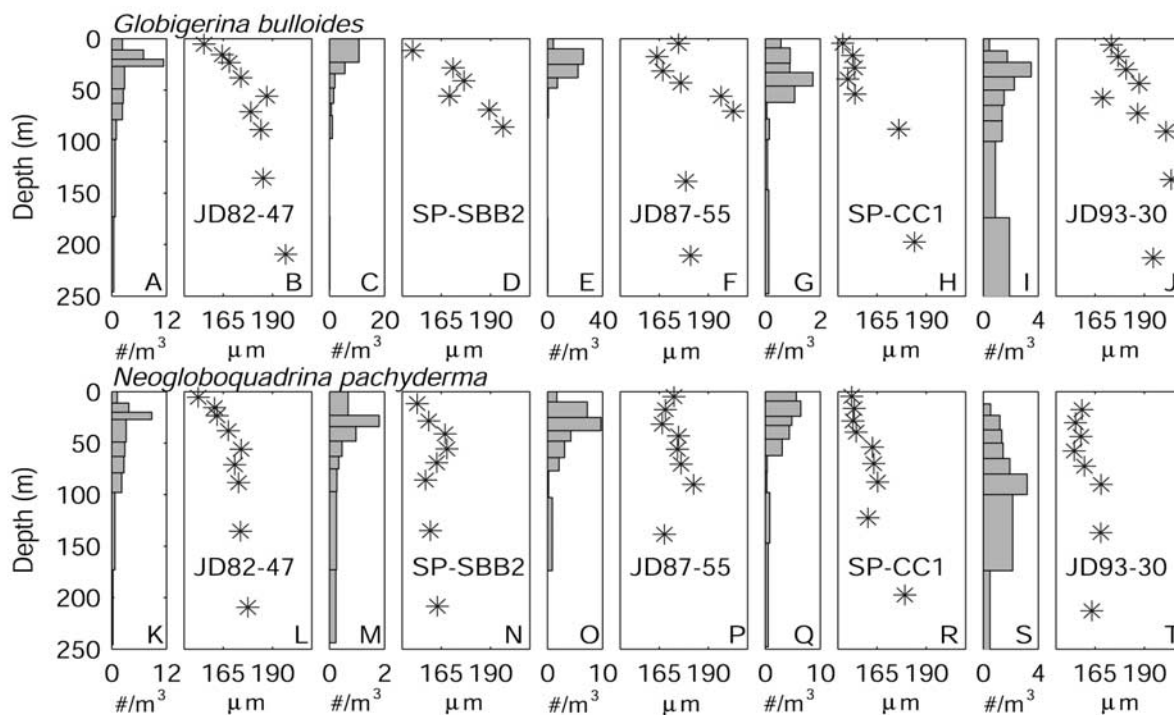

Figure 6. Vertical distributions of density and average size for (a–j) *G. bulloides* and (k–t) *N. pachyderma* from selected stations.

Figure 7. Comparison of the midpoint of day and night vertical distributions for (a) species with symbiotic algae and (b) the nonsymbiont (*G. bulloides*, *G. quinqueloba*, and *N. pachyderma*) and facultative symbiont-bearing species (*N. dutertrei*, *G. glutinata*, and *G. truncatulinoides*). Solid line shows the 1:1 relationship. Dotted line shows the average difference in pycnocline depth (10 m) between the day and night stations. See color version of this figure at back of this issue.

California Bight also had significant abundances of *G. bulloides* within and beneath the thermocline (Figure 4).

[31] *N. dutertrei* was well correlated with the depth of the 11.5°C isotherm (Figure 10f) but with a weaker slope than *N. pachyderma* and *G. truncatulinoides* (Table 3). The P-D intergrade had different relationships with the environmental variables than both *N. dutertrei* and *N. pachyderma*, but was more similar to *N. dutertrei* (Figure 10; Table 3). *G. truncatulinoides* had a strong response to the fluctuations of the 11.5°C isotherm, but the relationship was based on only nine stations (Figure 10i). Stations with <25 individuals counted also indicated a habitat within or beneath the thermocline for *G. truncatulinoides* (Figures 2, 3, and 4). While the amount of variance explained by the relationships of *N. pachyderma* with SST and other variables was modest and not statistically significant after correcting for multiple testing, the high slope of its relationship with the 11.5°C isotherm indicates a strong capacity to change depth with environmental change (Figure 10h; Table 3). The low slope of the relationship of *G. scitula* with the 11.5°C isotherm and high intercept reflect its weak relationship with environmental change and distinct preference for dwelling within or beneath the thermocline (Table 3; Figure 10e).

[32] *G. rubescens*, *G. siphonifera*, *G. falconensis*, *T. quinqueloba*, and *N. pachyderma* (sinistral) frequently had abundances too low to calculate core 25% intervals and/or had no relationship to the environmental variables listed in Table 2. However, when present in adequate abundances, these species were found both above and below the thermocline (Figures 2, 3, 4, and 5 and supplement).

3.5. Variations in Species Signatures and Stratification

[33] The effects of the aforementioned patterns of variability on species' temperature signatures is illustrated by comparing the weighted mean temperatures derived from the core 50% intervals of four species with SST (Figure 11a). Temperatures from the core 25% intervals are similar, while temperatures from the core 75% intervals or whole water column also result in similar patterns of variability, but with offsets toward lower temperatures at some stations. At SSTs around 15°C, *G. bulloides* frequently lives deeper and is less abundant. In such cases, *G. ruber* is more abundant and temperatures of the core 50% usually reflect SST. Conversely, at several stations where *G. ruber* is deeper and less abundant, temperatures from the core 50% of *G. bulloides* are more reflective of SST. Conditions where neither species reflects SST occur over the SBB in winter (JD81-49, JD82-47, nh82-47-1) and in the Bight in springtime and summer (SP-SDT1, NH90-35, and NH90-30). Over the SBB, there is strong isopycnal shoaling and most

Table 2. Relationships (r^2) Between Environmental Variables[a]

	SST	Pycnocline Depth	Chlorophyll *a* Maximum Depth	11.5 Isotherm Depth	33.6 Isohaline Depth	25.5 Isopycnal Depth
Pycnocline depth	0.00	–				
Chlorophyll *a* maximum depth	**0.48**	0.30	–			
11.5 isotherm depth	**0.39**	**0.36**	**0.85**	–		
33.6 isohaline depth	0.25	**0.35**	**0.65**	**0.73**	–	
25.5 isopycnal depth	0.30	**0.38**	**0.77**	**0.91**	**0.92**	–
Stratification	**0.97**	0.00	**0.42**	**0.33**	0.26	0.27

[a]Bold values indicate significant relationships (p < 0.05) after corrections for multiple testing by the Bonferroni criterion. All relationships are positive.

species are found within the chlorophyll maximum. In contrast, there is a separation of species' habitats at the more stratified Bight stations.

[34] Temperatures derived from the core 50% of *N. pachyderma* are often indicative of the upper thermocline (Figure 11a). However, the large vertical fluctuations of *N. pachyderma* can result in a range of derived temper-

atures. For clarity, temperatures derived from *O. universa*, *N. dutertrei* and *G. truncatulinoides* are not shown, but they generally reflect the upper thermocline or mixed layer. Temperatures from the core 50% of *G. scitula* consistently reflect subsurface conditions.

[35] Comparison of indices of stratification to measured thermal stratification illustrates that a more complex index is more reliable than a simple index (Figure 11b).

[36] The index of the near-surface dwelling species with the higher temperature signature in a given hydrographic condition (either *G. bulloides* or *G. ruber*) minus *G. scitula* (surf-Gs) closely follows measured stratification (Figure 11b). The simpler index (Gb-Np) shows a wide range of values across a small range of real differences in stratification in regions where both species are abundant (CC core, SBB, and Bight). Fluctuations in the habitat depth of *N. pachyderma* account for the range of values in the index when stratification is low. Conditions of higher stratification frequently have relatively lower Gb-Np values (NH77-100, SP-SDT1, JD93-30, JD30-30, NH90-30, NH 90-35) due to a downward shift in both *G. bulloides* and *N. pachyderma*.

4. Discussion

4.1. Factors Affecting Vertical Variability

[37] The different relationships of foraminiferal habitat depths with the depth of the 11.5°C isotherm and other environmental variables emphasize that each species has a different response to variations in hydrographic structure (Table 3). Variability in vertical distributions can confound interpretations of geochemical records from a single species. However, the combined geochemical records of several species can distinguish changes in species' habitat depth from changes in hydrography, since species differ in their response to variations in the depth of a particular isotherm and the depth of the thermocline. The general patterns of vertical distributions are discussed here, followed by the individual species-specific responses. I then discuss the effects of varying vertical distributions on geochemical signatures, observations from the sedimentary records, and implications of these results for reconstructing changes in hydrographic structure.
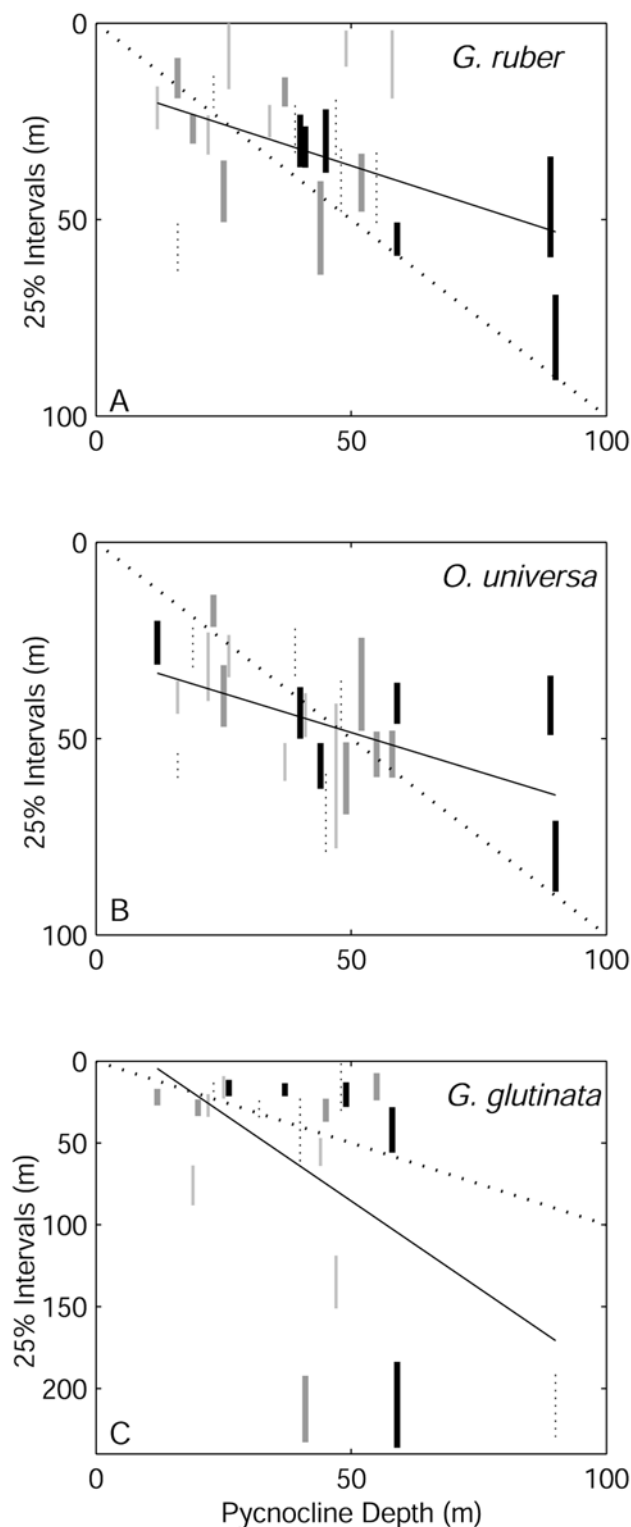

Figure 8. Vertical distributions of the core 25% of the population (vertical bars) versus depth of the pycnocline for (a) *G. ruber* (y = 0.42x + 15.3; r^2 = 0.24; p < 0.05), (b) *O. universa* (y = 0.40x + 28.6; r^2 = 0.29; p < 0.05), and (c) *G. glutinata* (y = 2.1x − 21.8; r^2 = 0.31; p < 0.05). Significance levels are corrected for multiple testing by the Bonferroni criterion. Thickness and shading of bars reflects quartiles of abundance of each species from all stations: Highest quartile (thick black), second highest quartile (thick gray), second lowest quartile (thin light gray), and lowest quartile (dotted). The dotted diagonal line indicates a 1:1 relationship with the pycnocline depth. Distributions above the dotted line lie within the mixed layer while distributions below the line are within or beneath the pycnocline.
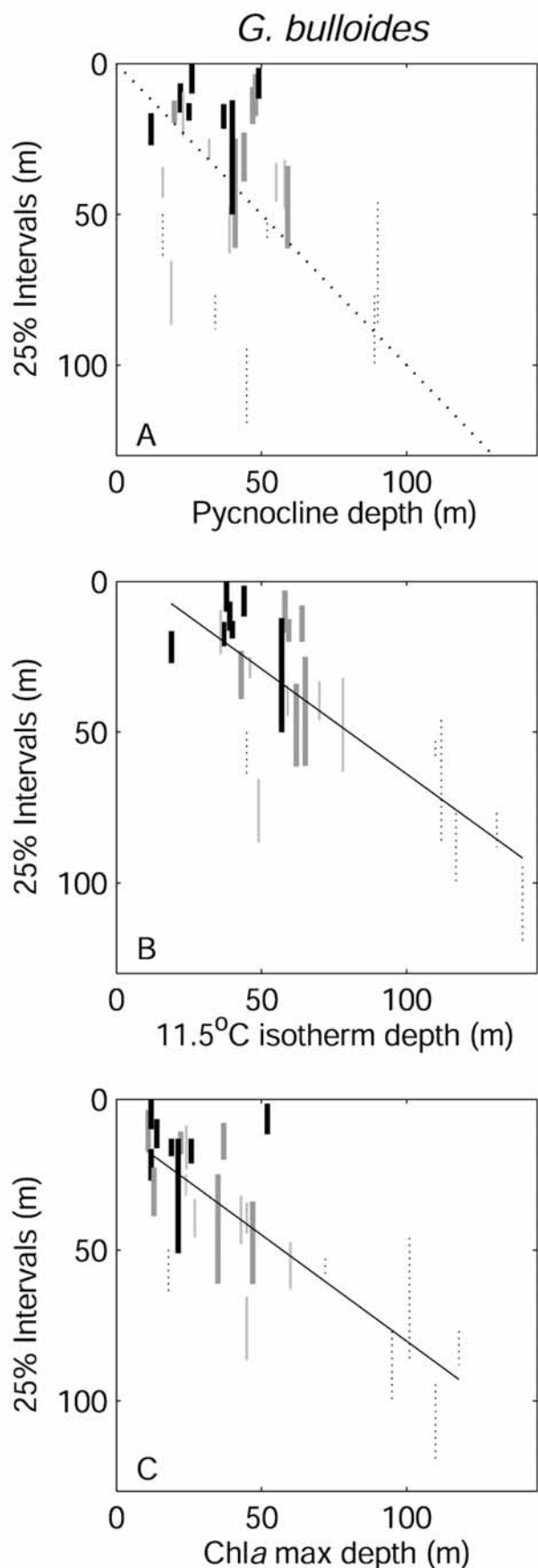
[38] It is notable that no species maintains a specific habitat depth exclusively within the mixed layer, within the thermocline, beneath the thermocline, or at a specific depth in the CCS. Most species can occur within or beneath the thermocline when it is shallow or when the chlorophyll maximum occurs within the thermocline, but occur within the mixed layer under other conditions. Concentrations of chlorophyll *a* are often similar between stations where many species are found either above or within the thermocline. Since light attenuation is positively related to chlorophyll concentrations in this region of the CCS [*Scripps Institution of Oceanography* (*SIO*), 2002], it is noteworthy that species with symbiotic algae frequently live within the thermocline where light levels are lower. Samples at shallow mixed layer stations generally had greater numbers of other zooplankton. Higher fertility may have a negative influence on foraminifera at these stations due to lower oxygen levels, changes in preferred light wavelength for symbionts, changes in preferred prey, or predation by zooplankton [*Berger*, 1971; *Bijma et al.*, 1992; *Oberhänsli et al.*, 1992].

[39] The relationships between foraminiferal habitat depths with the depth of the chlorophyll maximum may underestimate the importance of food availability. The vertical distribution of chlorophyll *a* about the chlorophyll maximum differs considerably between hydrographic conditions. Examination of Figures 2, 3, 4, and 5 reveals that the distribution of many species follows the distribution of chlorophyll *a* better than the depth of the chlorophyll maximum. Moreover, chlorophyll *a* is not likely to be an accurate predictor of true food availability.

[40] The increase in test size with depth is a well-documented pattern that results from dead foraminifera or the sinking of individuals from a preferred habitat [*Berger*, 1971; *Peeters et al.*, 1999]. That deeper tests can have shallower origins illustrates the importance of examining the core of the population as a measure of a species preferred habitat.

[41] Many different patterns of diel migrations have been proposed for planktonic foraminifera [*Boltovskoy*, 1973]. The occurrence and degree to which foraminifera may migrate vertically is not entirely resolved here. However, diel vertical migrations may occur on the scale of 10 m in symbiont-bearing species but do not appear to affect non-symbiont or facultative symbiont-bearing species in the CCS.

4.2. Species Specific Patterns

4.2.1. *Globigerinoides Ruber*

[42] *G. ruber* is considered to be one of the most reliable indicators of SST from tropical and subtropical regions as it generally lives within the mixed layer [*Ravelo and Fairbanks*, 1992]. However, moderate abundances at the base of the mixed layer or within the thermocline in the

Figure 9. Vertical distributions of the core 25% of the population (vertical bars) of *G. bulloides* versus (a) depth of the pycnocline, (b) depth of the 11.5°C isotherm (y = 0.70x − 5.4; r² = 0.64; p < 0.001), and (c) depth of the chlorophyll maximum (y = 0.70x + 9.8; r² = 0.66; p < 0.001). Details as in Figure 8.
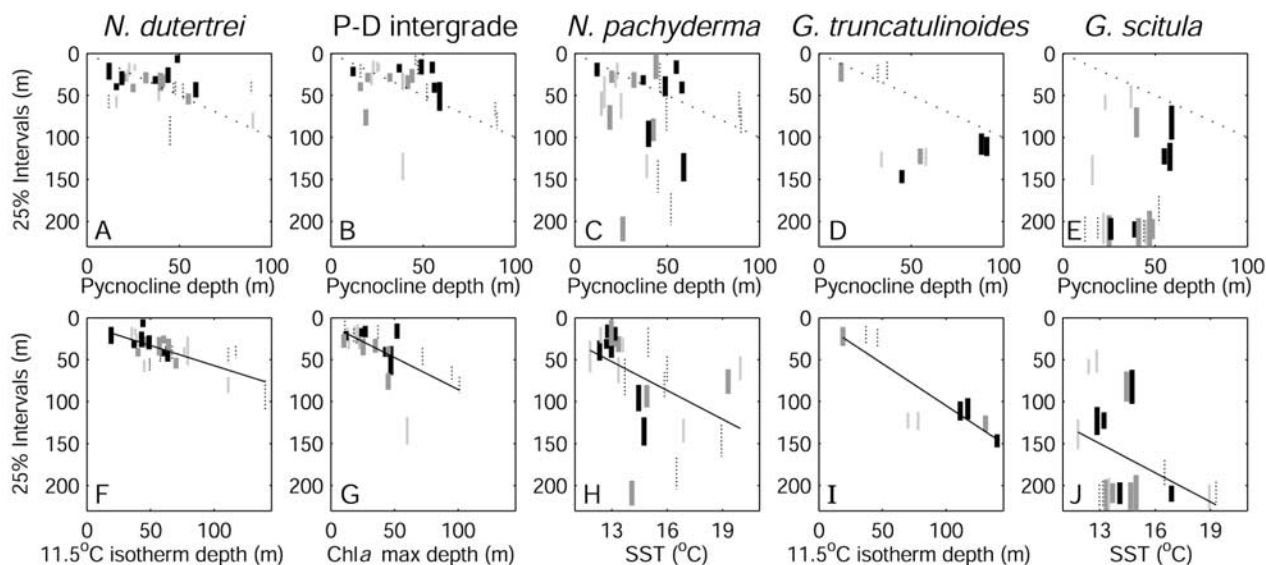
Figure 10. Vertical distributions of the core 25% of the population versus (a–e) depth of the pycnocline and (f–j) the variable with the most explanatory power for *N. dutertrei* ($y = 0.48x + 8.7$; $r^2 = 0.57$; $p < 0.001$), PD-intergrade ($y = 0.76x + 9.4$; $r^2 = 0.45$; $p < 0.001$), *N. pachyderma* ($y = 11.43x - 96.4$, $r^2 = 0.23$; $p = 0.06$), *G. truncatulinoides* ($y = 1.0x + 4.7$; $r^2 = 0.75$; $p < 0.05$), and *G. scitula* ($y = 11.6x - 1.23$, $r^2 = 0.16$; $p = 0.40$). Details as in Figure 8.

CCS indicate that it will not always be indicative of SST. Greater overlap with potential food availability than maximum light availability is not surprising since *G. ruber* is omnivorous and it is unclear how symbionts benefit their host [*Hemleben et al.*, 1989]. Nonetheless, a low slope of the response to a deepening isotherm makes *G. ruber* ideal for recording near-surface conditions when other species dwell deeper.

4.2.2. *Globigerina Bulloides*

[43] Since *G. bulloides* is frequently used in sedimentary analyses and is generally assumed to represent SSTs, it is important to distinguish living in the near surface from living in the mixed layer. Observations of high abundances of *G. bulloides* near the surface when isotherms are shallow and low abundances in deeper depths with a deeper chlorophyll maximum are consistent with many other studies [*Fairbanks and Wiebe*, 1980; *Sautter and Thunell*, 1991a; *Ortiz et al.*, 1995; *Peeters and Brummer*, 2002]. However, high abundances of *G. bulloides* near the surface but within a subsurface chlorophyll maximum beneath the mixed layer have not been previously emphasized. Observations of the present study indicate that under some conditions *G. bulloides* can occur in high abundances near the surface but in temperatures well below SST.

[44] The populations of *G. bulloides* occurring well beneath the thermocline in moderate abundances are likely to be a different genotype or be in a different phase of life history since they have a dramatic shift in the average size with depth and I observed differences in morphology. The forms found deeper are more compact, have smaller apertures and are similar to those described by others [*Sautter and Thunell*, 1991a; *Bemis et al.*, 2002]. The three obvious

Table 3. Relationships (r^2) Between the Median Depth of Species With More Than Eight Core 25% Intervals Calculated and Selected Environmental Corrections for Multiple Testing by the Bonferroni Criterion[a]

Species	SST	Pycnocline Depth	Chlorophyll *a* Maximum Depth	11.5 Isotherm Depth	Relationship to 11.5 Isotherm
G. ruber	0.00	**0.24**	0.04	0.08	$y = 0.16x + 22$
O. universa	0.00	**0.29**	0.18	0.20	$y = 0.23x + 31$
G. glutinata	0.13	**0.31**	0.19	0.13	$y = 0.91x + 10$
G. bulloides	**0.48**	0.13	**0.66**	**0.64**	$y = 0.70x + 10$
N. dutertrei	0.16	0.18	**0.41**	**0.56**	$y = 0.48x + 9$
P-D intergrade	**0.39**	0.10	**0.45**	0.31	$y = 0.63x + 0$
N. pachyderma	0.23	0.02	0.15	0.19	$y = 0.80x + 20$
G. truncatulinoides	0.37	0.29	0.52	**0.75**	$y = 1.00x + 5$
T. quinqueloba	0.10	0.01	0.00	0.05	$y = 1.00x + 19$
G. scitula	0.16	0.04	0.01	0.02	$y = 0.31x + 148$
G. siphonifera	0.01	0.02	0.01	0.03	$y = 0.30x + 52$

[a]The regression relationship of each selected species to the depth of the 11.5 isotherm is also shown. All relationships are positive.
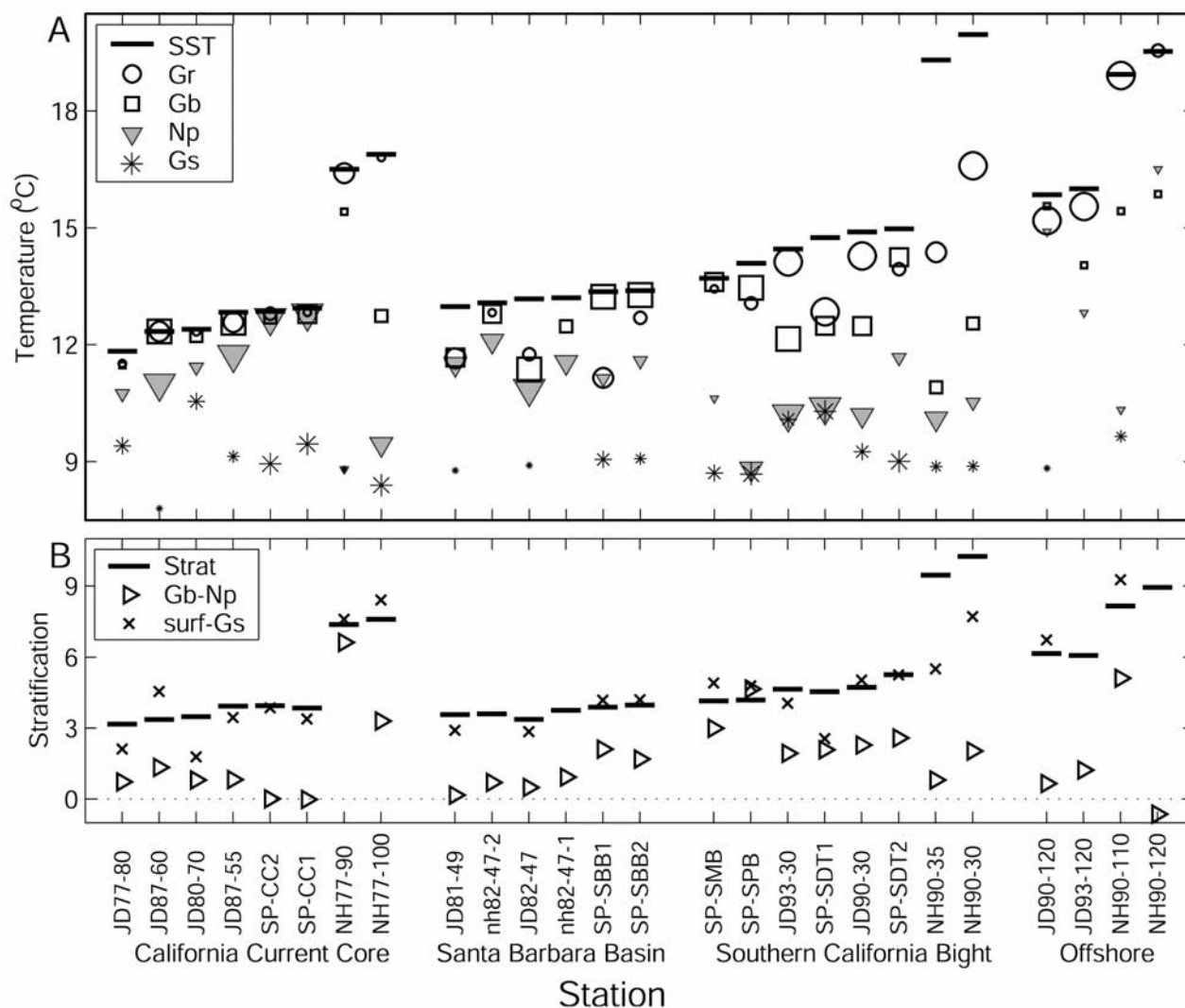
Figure 11. (a) Summary of measured SST and weighted mean temperature of the core 50% of four species of foraminifera indicating variability in temperature signatures by region and sampling station (*G. bulloides*, Gb; *G. rubber*, Gr; *N. pachyderma*, Np; and *G. scitula*, Gs). (b) Measured thermal stratification (0–150 m) and two foram-derived indices of stratification. The Gb-Np index is the difference between weighted mean temperature of *G. bulloides* and *N. pachyderma*. The surf-Gs index is the difference between whichever near surface dweller provides a higher temperature index (either *G. bulloides* or *G. ruber*) and *G. scitula*. Sizes of symbols in Figure 11a are proportional to quartiles of abundance as in Figure 8. Winter stations are JD and nh. Summer stations are NH. Spring stations are SP. See color version of this figure at back of this issue.

cases occur within the Southern California Bight during winter and spring, similar times of year as the observations by *Sautter and Thunell* [1991a]. The deeper dwelling morphology appears to be a consistent aspect of the *Globigerina bulloides* species complex that has higher $\delta^{18}O$ values and can significantly affect $\delta^{18}O$ time series [*Bemis et al.*, 2002].

4.2.3. Orbulina Universa

[45] Observations that *O. universa* varies its mode of vertical distribution both above and within the thermocline is consistent with many other studies [*Sautter and Thunell*, 1991a; *Ravelo and Fairbanks*, 1992; *Ortiz et al.*, 1995]. The

lower slope of the relationship of *O. universa* to the 11.5°C isotherm (Table 3) relative to other species may be of particular use in determining when other species are changing habitat depth to follow a deepening isotherm. The regions where *O. universa* occurs in the mixed layer generally have deeper thermocline depths (Figure 8b) and may correspond to different genotypes since *de Vargas et al.* [1999] found different genotypes in different hydrographic regimes.

4.2.4. Neogloboquadrina Dutertrei

[46] Covariation of *N. dutertrei* with the depth of a given isotherm, either within or beneath the thermocline, is a

consistent observation within the CCS [*Sautter and Thunell*, 1991a; *Ortiz et al.*, 1995]. *N. dutertrei* can be largely herbivorous [*Hemleben et al.*, 1989], thus its occurrence below significant concentrations of chlorophyll *a* when the thermocline is shallow may be associated with a change in food type preference. The larger average test sizes in the Bight in summer likely indicate greater viability since the shallow thermocline, higher SSTs, and subsurface chlorophyll maximum typify the preferred habitat of *N. dutertrei* [*Sautter and Thunell*, 1991a; *Ravelo and Fairbanks*, 1992].

4.2.5. *Neogloboquadrina Pachyderma* (Dextral)

[47] As *N. pachyderma* experiences strong seasonality in its preferred temperate and polar environments [*Vincent and Berger*, 1981], it likely developed different life history strategies that make it readily adaptable to different food and temperature ranges. Highest abundances of *N. pachyderma* within the mixed layer and chlorophyll maximum in the CC core (Figure 2) are consistent with observations at higher latitudes in the CCS and other high latitude locations [*Ortiz et al.*, 1995; *Mulitza et al.*, 1997; *Mortyn and Charles*, 2003]. *N. pachyderma* has also been found beneath the thermocline and significant chlorophyll levels within the Southern California Bight [*Sautter and Thunell*, 1991a]. Since SST differs little between some of these observations, *N. pachyderma* may be changing preferred foods types in response to food availability. Different vertical distributions could also reflect different genotypes since *N. pachyderma* (dex) is a species complex made up of at least several genotypes within the dextral coiling morphology [*Darling et al.*, 2000; *Bauch et al.*, 2003]. The existence of multiple genotypes reinforces the importance of distinguishing the PD-intergrade.

4.2.6. PD-Intergrade

[48] The smaller average size of the PD-intergrade indicates the possibility that they could be less developed individuals of *N. dutertrei*, which would have little effect on the observed patterns of vertical distribution. Similar patterns of vertical distribution between the PD-intergrade and *N. dutertrei* are consistent with a study off northern California that combined these identities based on their similar distributions [*Ortiz et al.*, 1995]. On the basis of the significantly greater fluxes of *N. pachyderma* than *N. dutertrei* [*Sautter and Thunell*, 1991b; *Kincaid et al.*, 2000; *Black et al.*, 2001], many individuals of the PD-intergrade were probably considered *N. pachyderma* in these sediment trap studies examining mature individuals. That the average test size of the PD-intergrade is similar to *N. pachyderma* indicates that incomplete morphological development is less likely to account for designation of PD-intergrade by individuals of *N. pachyderma*. However, combination of the PD-intergrade with *N. pachyderma* would have altered the results of the present study. *N. pachyderma* would have more similar patterns to those of the PD-intergrade, including a decrease in the magnitude of variability in habitat depth better explained by environmental variables. Different genotypes is a real possibility.

4.2.7. *Globorotalia Truncatulinoides*

[49] A preferred habitat of *G. truncatulinoides* in the upper thermocline in the CCS implies that *G. truncatulinoides*, or some of its genotypes, may not always be as reliable an indicator of conditions beneath the thermocline as it is in other regions [*Mulitza et al.*, 1997; *Mortyn and Charles*, 2003]. While *G. truncatulinoides* occurs deeper than 250 m in other regions [*Mulitza et al.*, 1997], there is rarely a maximum in density observed in the deepest stratum sampled here, suggesting that the core of the population was usually sampled. However, secretion of a large portion of calcite while sinking could account for part of the discrepancy [*Mulitza et al.*, 1997]. Individuals from the offshore region are more conical in shape and may correspond to species 1 or 2, based on descriptions of morphology and subtropical preferences of these genotypes [*de Vargas et al.*, 2001]. Varieties found at other stations are more compressed and may correspond to species 3 or 4 [*de Vargas et al.*, 2001].

4.2.8. *Globorotalia Scitula*

[50] Although *G. scitula* may vary its distribution between the upper and lower thermocline, it is generally most abundant well below the thermocline in this part of the CCS, in the northern regions of the CCS [*Ortiz et al.*, 1996], and other locations [*Oberhänsli et al.*, 1992; *Itou et al.*, 2001]. Since highest abundances are often in the deepest stratum sampled, peaks in abundance may occur deeper than sampled.

4.3. Factors Affecting Expected Geochemical Signatures

[51] Since each tow is a snapshot in time and may not reflect all processes of test production and calcification, it is important to consider whether geochemical signatures would vary with the observed patterns of distribution. Foraminiferal $\delta^{18}O$ values largely reflect the depths at which abundances are high and test sizes are below maximum values [*Peeters and Brummer*, 2002]. However, the addition of calcite during gametogenesis and/or while sinking can also contribute to $\delta^{18}O$ signatures [*Duplessy et al.*, 1981; *Bauch et al.*, 1997; *Mortyn and Charles*, 2003]. Different patterns of test size and abundance with depth indicate that there may be species-specific differences in the extent to which calcification occurs throughout the water column. Sediment trap studies integrate processes of calcification occurring in time and depth and thus provide a context for understanding how some populations in the CCS acquire $\delta^{18}O$ signatures.

[52] Sediment trap studies indicate that both *G. bulloides* and *N. pachyderma* can acquire $\delta^{18}O$ signatures from different parts of the water column [*Sautter and Thunell*, 1991a]. Individuals of *G. bulloides* collected over the San Pedro Basin in early spring had the compact morphology and lived around 100 m, well beneath the thermocline, whereas samples from upwelling conditions indicate a mixed layer signature [*Sautter and Thunell*, 1991a; *Spero and Lea*, 1996]. Over the SBB, $\delta^{18}O$ values reflect the species-specific predicted calcite values for *G. bulloides* at 20 m, or below that depth, better than those at the surface [*Pak and Kennett*, 2002], but do track seasonal and interannual fluctuations of SST [*Thunell et al.*, 1999; *Friddell et al.*, 2002]. Comparison of $\delta^{18}O$ values from *G. bulloides* and *N. pachyderma* in a deep trap (470 m) with those from a trap at 65 m below the surface indicates that both species
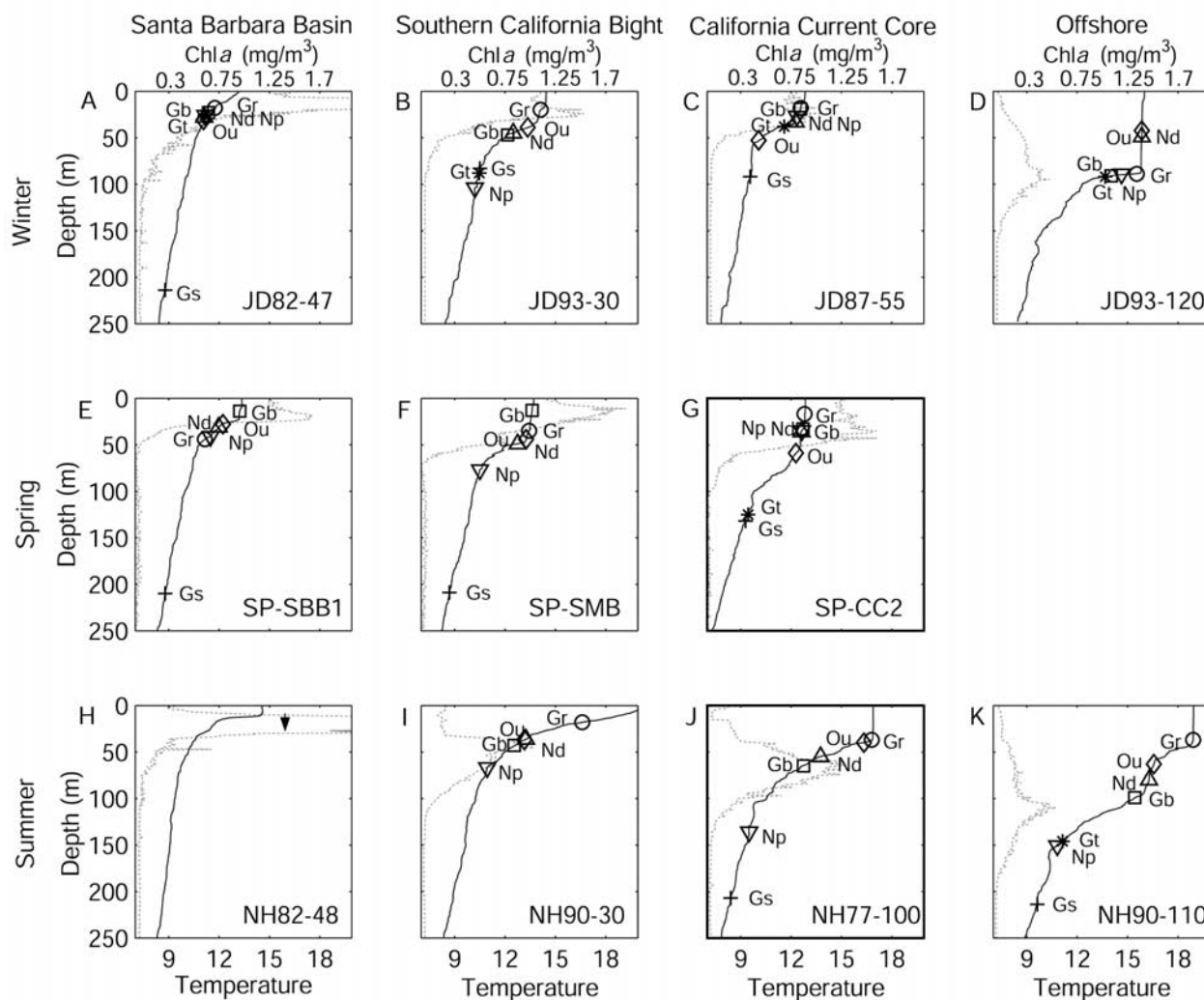
Figure 12. Variability of habitat depth and associated temperature (solid line) and chlorophyll *a* (dotted line) of the core 50% of the population for the principal species of this study (*G. bulloides*, Gb; *G. rubber*, Gr; *O. universa*, Ou; *N. dutertrei*, Nd; *N. pachyderma*, Np; *G. truncatulinoides*, Gt; and *G. scitula*, Gs). One representative station is illustrated for each hydrographic region and season. The offshore region was not sampled during spring. Arrow at the SBB station in summer indicates that each foraminiferal species was more abundant within or beneath the chlorophyll maximum than in the mixed layer. See color version of this figure at back of this issue.

acquire a portion of their $\delta^{18}O$ signature from below 65 m [*Pak and Kennett*, 2002]. The 65 m samples consistently had lighter $\delta^{18}O$ values than the deeper trap, although the difference was much greater for *N. pachyderma* [*Pak and Kennett*, 2002, Figure 4]. Figure 2 suggests that the greater offset in *N. pachyderma* results from a greater portion of its population living below 65 m. Although *N. pachyderma* predominantly has a signature from the thermocline, it can acquire a $\delta^{18}O$ signature similar to *G. bulloides* and be indicative of the mixed layer [*Sautter and Thunell*, 1991a; *Pak and Kennett*, 2002; *Friddell et al.*, 2002]. While the flux of *N. pachyderma* to the San Pedro Basin trap was low when it lived in the mixed layer, this study shows that abundances can be high in the mixed layer.

[53] Previous sediment trap studies and the vertical distribution patterns presented here indicate that $\delta^{18}O$ signatures are acquired from different depths. Geochemical signatures from foraminifera in the CCS can be expected to vary with changes in hydrographic structure as illustrated in Figure 12. Paleoceanographic studies using planktonic foraminifera from ocean sediments should distinguish changes in depth from direct changes in temperature and water composition occurring in the water column.

4.4. Application to Paleoceanographic Records

[54] Patterns of foraminiferal distributions found here can lead to improved understanding of sedimentary $\delta^{18}O$ records in relation to changes in ocean climate. A multi-decadal warming of $1-1.5°C$ occurred in the CCS since
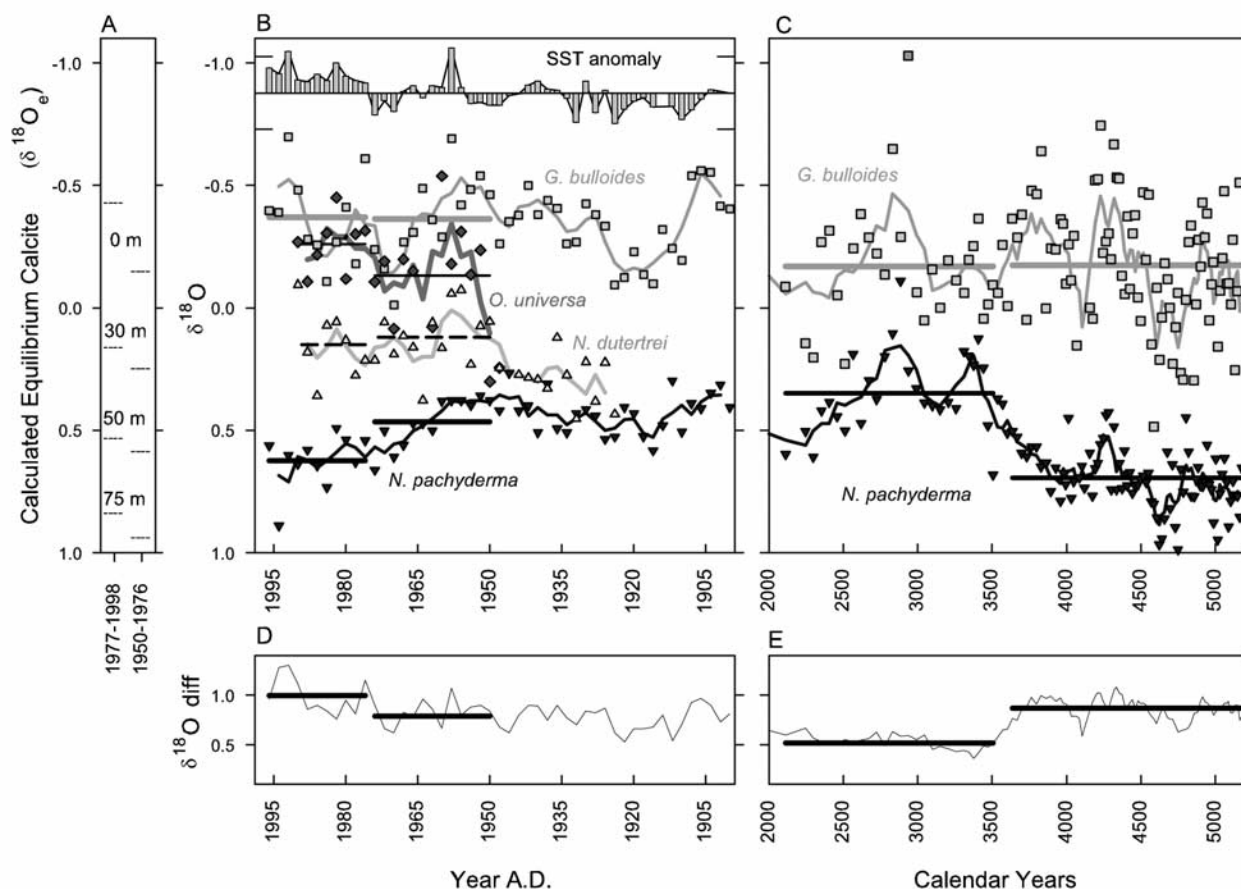
Figure 13. Comparison of downcore isotopic records from the Santa Barbara Basin (SBB) sediments and hydrographic measurements illustrating different time intervals where changes in foraminifera $\delta^{18}O$ depart from expectations for a single depth. (a) Calculated equilibrium calcite values ($\delta^{18}O_e$) at several depths from CalCOFI hydrographic data for the periods 1949–1976 and 1977–1998 [*Field and Baumgartner*, 2000]. (b) The 20th century $\delta^{18}O$ records of *G. bulloides* and *N. pachyderma* in 2-year intervals from *Weinheimer et al.* [1999], together with measurements from *N. dutertrei* and *O. universa* (Field et al., unpublished data, 2002) using the approach described in the work of *Field and Baumgartner* [2000] but using 2-year intervals. Also shown in Figure 13b are normalized SST anomalies from Comprehensive Ocean-Atmospheric Data Set (COADS) data off the west coast of North America, extending from Canada to northern Baja California. (c) The mid-Holocene record from *Friddell et al.* [2003] with measurements every 13–52 years (from 5200 to 2000 years before present). In Figures 13b and 13c varying lines show three point running averages for clarity. Horizontal bars are the average values of all measurements within a selected time interval. Ordinate axis is inverted in Figures 13a–13c to be consistent with changes in temperature. The lower $\delta^{18}O_e$ values at fixed depths over the SBB in 1977–1998 relative to 1950–1976 are not observed in the records of *G. bulloides*, *N. pachyderma*, or *N. dutertrei*. (d) Stratification index and (e) from the difference in each $\delta^{18}O$ value between *G. bulloides* and *N. pachyderma* (thin line) and the average of the index for each chosen period (bold horizontal bar). See color version of this figure at back of this issue.

1977 with largest anomalies at the surface, caused by changes in ocean-atmosphere heat flux [*Roemmich and McGowan*, 1995; *Di Lorenzo et al.*, 2004]. CalCOFI records of temperature and salinity over the SBB permit calculations of equilibrium calcite values ($\delta^{18}O_e$) by depth, which are averaged across the decadal periods 1950–1976 and 1977–1998 (Figure 13a) [*Field and Baumgartner*, 2000]. Changes in $\delta^{18}O_e$ were strongest near the surface, largely unaffected by changes in salinity, and are of the same sign at fixed depths between the decadal time intervals. The temporal component of SST anomalies is shown in Figure 13b.

[55] From Figure 13a, lower $\delta^{18}O$ values are expected (not considering changes in habitat depth) for all species during the warmer decades. A larger $\delta^{18}O$ decrease in *G. bulloides* relative to the deeper dwelling *N. pachyderma* is also expected due to greater warming near the surface. This should result in an increase in a commonly used stratification index ($\delta^{18}O$ *G. bulloides* – *N. pachyderma*).

[56] The δ^{18}O records of *G. bulloides* and *N. pachyderma* from the SBB (see Figure 1 for location) do not track the warming in the expected way [from *Weinheimer et al.*, 1999, Figure 13b]. Although δ^{18}O of *G. bulloides* reflects much of the variation in SST over the last 100 years, there was no change in average δ^{18}O between the periods 1950–1976 and 1977–1998. There is an unexpected increase in δ^{18}O values of *N. pachyderma* between these periods, indicating it lived in colder waters in more recent decades. The increase in δ^{18}O values of *N. pachyderma* results in an increase in the δ^{18}O stratification index in response to the mid-1970s warming (Figure 13d), but not through the expected mechanism.

[57] The best explanation for the mismatch between the δ^{18}O records and ocean observations (Figure 13b) is that the warming resulted in a downward shift in isotherms, chlorophyll concentrations, and the habitat depths of both *G. bulloides* and *N. pachyderma*. If the average δ^{18}O signature of *G. bulloides* derives from approximately 20 m depth within the warm period of 1977–1998 [*Pak and Kennett*, 2002], then an average signature coming from 10 m in the preceding decades could account for the lack of δ^{18}O change between time periods. The $\delta^{18}O_e$ value at 20 m (−0.11) from 1977–1998 is similar to the value at 10 m (−0.07) from 1950–1977 [*Field and Baumgartner*, 2000]. A shift in habitat depth of approximately 25 m for *N. pachyderma* is needed to explain the heavier δ^{18}O values during the warmer decades, which is well within the range of observations shown in Figure 10c.

[58] Alternatively, there may have been a shift in the production of tests of either species toward colder seasons during the warmer decades. The biweekly sediment trap collections show considerable variability in test flux between sampling periods, seasons and years, but do not indicate a season of preferred flux for these species [*Kincaid et al.*, 2000; *Black et al.*, 2001]. High fluxes occur at all times of the year for *G. bulloides* and in spring, summer, and fall for *N. pachyderma*. Since there are no clear seasonal signals in test flux, there is little potential for a seasonal bias in δ^{18}O values to result from changes in test flux. Furthermore, *Friddell et al.* [2002] found little difference (<0.05 permil) between averaged flux-weighted δ^{18}O values and averaged δ^{18}O values for these species in comparing months and years with distinctive patterns of test flux.

[59] The interpretations of the decadal changes resulting from changes in habitat depths are corroborated by δ^{18}O series from two other species. δ^{18}O of *N. dutertrei* indicates a slight cooling across the 1977 warming (Figure 13b), consistent with the observation that *N. dutertrei* follows the depth of a given isotherm but does not change depth as much as *N. pachyderma* (Table 3). Records of *O. universa* indicate a moderate warming coincident with the shift, which is consistent with an upper thermocline or mixed layer habitat that varies considerably less with the depth of an isotherm than *G. bulloides*, *N. dutertrei*, and *N. pachyderma* (Table 3). The different responses between these species to the increase in stratification emphasizes the importance of obtaining records from multiple species to obtain information on water column structure and constrain possible interpretations.

[60] Shifts in species' habitat depth likely affect many other δ^{18}O records. *Friddell et al.* [2003] found that the mid-Holocene period of 5200–3600 has the highest stratification index and greatest centennial-scale variability in a Holocene record from the SBB. Figure 13c shows that the average δ^{18}O values of *G. bulloides* did not change between two millennial intervals (5200–3600 and 3600–2000) of different inferred stratification (Figure 13e). The average millennial change in *N. pachyderma* (0.35) is twice the difference observed between the different decadal periods (0.17). The mid-Holocene change of 0.35 permil would correspond to a temperature change of approximately 1.5°C, or a depth change of approximately 30–50 m (depending on changes in $\delta^{18}O_e$ in the water column). It would be difficult for a change of 1.5°C to occur within the thermocline with no change in the near surface, while vertical shifts greater than 30–50 m occur in *N. pachyderma* (Figure 10c).

[61] The different millennial intervals appear analogous to the different decadal periods of the late 20th century in that the increase in the stratification index and inferred ocean warming from 5200–3600 may have resulted in deeper habitat depths for both species. Alternatively, changes may be due entirely to shifts in *N. pachyderma*. *N. pachyderma* occurs in the mixed layer in core California Current waters that have the same degree of stratification as upwelling times (spring) in the Southern California Bight or over the SBB, where it occurs within the thermocline (Figures 11a, 12c, 12e, 12f, and 12g). Although additional records are needed to elucidate the mechanisms of change, the SBB region may have experienced greater influence of California Current waters and less coastal upwelling during the period of 3600–2000.

[62] Observations of vertical distributions offer speculation of mechanisms of change occurring on longer time-scales as well. Stadial periods over the SBB are characterized by high but similar δ^{18}O values in *G. bulloides* and *N. pachyderma*, which reflect cool conditions, little stratification, and similar habitats of these two species [*Hendy and Kennett*, 1999]. Warmer interstadial periods during the last glacial show a relatively greater decrease in δ^{18}O values in *G. bulloides* than *N. pachyderma*. Although the decrease in δ^{18}O in both species clearly indicates greater stratification during interstadials, *N. pachyderma* has the capacity to live in the mixed layer like *G. bulloides*, particularly within the California Current core (Figures 12c and 12g). Observations summarized in Figures 12e and 12f suggest that greater isopycnal shoaling from coastal upwelling are associated with a deeper habitat of *N. pachyderma* than *G. bulloides*. Thus interstadial periods may be associated with both conditions of near-surface warming and greater isopycnal shoaling (from increased upwelling) due to a stronger continental low-pressure system. Lower temperatures during stadial periods may be associated with deeper mixed layers from reduced coastal upwelling and greater influence of the flow of the California Current along the coast. Such conditions would result from strengthening of the Aleutian Low (and higher pressure over the continent), which deepens isopycnals along the coast [*Miller*, 1996].

[63] Foraminiferal records of climatic changes from the Holocene have reduced amplitudes relative to longer timescales and may be particularly susceptible to changes in habitat depth. However, low estimates of changes in SST from δ^{18}O records in the tropics during the Last Glacial Maximum emphasize the importance of identifying potential biases and accounting for changes in habitat depth on all timescales [*Stott and Tang*, 1996; *Patrick and Thunell*, 1997].

4.5. Implications for Reconstructing Hydrographic Structure

[64] Greater insight into the mechanisms of climatic change may come from reconstructing the thermal structure of the water column (both depth and intensity of the thermocline) rather than just the difference in temperature across the thermocline (e.g., surf-Gs index). For example, stations SP-CC1 and SP-CC2 have considerably deeper mixed layers than SBB stations but similar degrees of thermal stratification (Figures 11a, 12a, 12c, 12e, and 12g). These different hydrographic conditions and associated changes in habitat depth of *N. pachyderma* may represent important differences between the influence of the California Current and coastal upwelling through time over the SBB. The δ^{18}O difference between *G. bulloides* and *N. pachyderma* is the most commonly used stratification index from the CCS [*Hendy and Kennett*, 1999; *Friddell et al.*, 2002, 2003] and reflects changes in stratification across the annual cycle over the SBB [*Pak and Kennett*, 2002; *Friddell et al.*, 2002]. The inadequacy of the Gb-Np index as a measure of stratification here (Figure 11b) is a consequence of the wider range of hydrographic conditions sampled, which captured greater variations in habitat depths.

[65] Determining changes in temperatures from the upper thermocline and below it is best done through multiple species. The different responses of *N. pachyderma*, *N. dutertrei*, and *O. universa* to the deepening of an isotherm signify that relative differences in their acquired signatures can reflect the deepening of isotherms. In contrast, shared variability in signatures of all species would likely reflect real changes in temperature within the thermocline. Therefore determining whether signatures of *N. pachyderma* reflect a deeper habitat or lower temperatures can be achieved by comparison with *O. universa* or *N. dutertrei*, which do not vary depth as much as *N. pachyderma*. However, these three species live in the mixed layer at times (Figures 8b, 10a, and 10c). *G. scitula* consistently lives below the thermocline and would be particularly useful in evaluating the possibility of other species living in the mixed layer.

[66] Relative differences in δ^{18}O values between *G. bulloides* and *G. ruber* (or *O. universa*) may reflect changes in hydrography that cause one species to live deeper and not reflect SST. Temperature signatures from *G. bulloides* may underestimate SST when isotherms are shallow but high chlorophyll concentrations occur across a thermal gradient. Likewise, a symbiont bearing species can occur at the base of the mixed layer or upper thermocline where temperatures are lower than SST. The moderate responses of *G. ruber*, and *O. universa* to a deepening of an

isotherm suggest that even if no species reflects SST, the relative difference between these species and *G. bulloides* can reflect variations in stratification. A deepening of isotherms could also result in greater separation in depth between other species.

[67] Variations in species assemblages (or other paleoceanographic proxies) may be useful in determining whether variations in the geochemical signature of a given species are due to variations in habitat depth since assemblages are affected by hydrographic structure as well [*Sautter and Thunell*, 1991a, 1991b; *Ravelo and Fairbanks*, 1992; *Watkins and Mix*, 1998]. For example, the species assemblage was dominated by *N. pachyderma* where it lived in the mixed layer (SP-CC1, SP-CC2). In contrast, the assemblage was a more even mixture of *G. ruber*, *G. bulloides*, and *N. pachyderma* where *N. pachyderma* lived well below the thermocline (SP-SDT1, JD93-30, JD90-30). Note that if the signature from *G. bulloides*, or another species, is derived from the thermocline due to a subsurface chlorophyll maximum, an alkenone unsaturation index from coccolithophorids could acquire the same subsurface temperature signature. While the results of this study question the reliability of geochemical records from one or two species, they provide a basis for reconstructing hydrographic structure and determining the mechanisms of climatic change.

5. Conclusions

[68] Vertically stratified plankton samples taken from diverse hydrographic conditions provide a basis for understanding which environmental properties are most important in determining habitat depths of planktonic foraminifera. Each species examined shows considerable variability in habitat depth and is abundant in different positions of the water column relative to a fixed depth beneath the surface and relative to the thermocline (e.g., above, within, or below the thermocline). Consequently, changes in climate recorded in geochemical signatures could be confounded by changes in habitat depth. However, the species-specific responses to changes in hydrographic structure result in some expected patterns of change. Records from multiple species can distinguish true temporal changes in hydrographic structure from shifts in the vertical position in the water column of a single species.

[69] *G. ruber* varies less than other species with respect to depth below the surface. It can occur within the pycnocline when the pycnocline is shallow. When the pycnocline is deeper and SST is higher, *G. ruber* occurs within the mixed layer and is the best indicator of near-surface conditions.

[70] *G. bulloides* tracks the depth of the chlorophyll maximum and the 11.5°C isotherm. *G. bulloides* is the best indicator of near-surface conditions when isotherms are shallow and chlorophyll concentrations are high. High abundances can occur both in the mixed layer and the upper thermocline.

[71] *O. universa*, *N. dutertrei*, and *G. truncatulinoides* occur in the mixed layer and the thermocline but are primarily found within the upper thermocline. Like *G. ruber*, *O. universa* shows relatively little change in

habitat depths. In contrast, *N. dutertrei* and *G. truncatulinoides* follow isotherms and the depth of the chlorophyll maximum more closely and have a greater capacity for vertical shifts in habitat.

[72] *N. pachyderma* generally lives within the upper thermocline but has considerable variability in habitat depth, ranging from the mixed layer to the deeper thermocline, which is difficult to attribute to specific environmental factors. *N. pachyderma* can be inferred to have acquired a signature from deeper depths through comparison with records from *N. dutertrei* or *O. universa*.

[73] *G. scitula* is consistently most abundant within or beneath the thermocline and is the preferred species for assessing subsurface conditions. The relative differences in geochemical signatures between *G. scitula* and other thermocline dwelling species can indicate when other species have acquired a geochemical signature from the mixed layer.

[74] Examination of $\delta^{18}O$ records from Santa Barbara Basin sediments confirms that changes in habitat depth are identifiable based on the records of multiple species and the species-specific predicted responses to well observed decadal changes. Increasingly more accurate interpretations of geochemical records can be made by using multiple species and formulating expectations of their patterns of change.

References

Bauch, D., J. Carstens, and G. Wefer (1997), Oxygen isotope composition of living *Neogloboquadrina pachyderma* (sin.) in the Arctic Ocean, *Earth Planet. Sci. Lett.*, 146, 47–58.

Bauch, D., K. Darling, J. Simstich, H. A. Bauch, H. Erlenkeuser, and D. Kroon (2003), Palaeoceanographic implications of genetic variation in living North Atlantic *Neogloboquadrina pachyderma*, *Nature*, 424, 299–302, doi:10.1038/nature01778.

Bemis, B. E., H. J. Spero, and R. C. Thunell (2002), Using species-specific paleotemperature equations with foraminifera: A case study in the southern California Bight, *Mar. Micropaleontol.*, 46, 405–430.

Berger, W. H. (1971), Sedimentation of planktonic foraminifera, *Mar. Geol.*, 11, 325–358.

Berger, W. H., and J. S. Killingley (1977), Glacial-Holocene transition in deep-sea carbonates: Selective dissolution and the stable isotope signal, *Science*, 197, 563–566.

Bijma, J., W. W. Faber Jr., and C. Hemleben (1990), Temperature and salinity limits for growth and survival of some planktonic foraminifers in laboratory cultures, *J. Foraminiferal Res.*, 20, 95–116.

Bijma, J., C. Hemleben, H. Oberhänsli, and M. Spindler (1992), The effects of increased water fertility on tropical spinose planktonic foraminifers in laboratory cultures, *J. Foraminiferal Res.*, 22, 242–256.

Black, D. E., R. C. Thunell, and E. J. Tappa (2001), Planktonic foraminiferal response to the 1997–1998 El Niño: A sediment-trap record from the Santa Barbara Basin, *Geology*, 29, 1075–1078.

Boltovskoy, E. (1973), Daily vertical migration and absolute abundance of living planktonic foraminifera, *J. Foraminiferal Res.*, 3, 89–94.

Brink, K. H., and T. J. Cowles (1991), The Coastal Transition Zone Program, *J. Geophys. Res.*, 96, 14,637–14,647.

Caron, D. A., A. W. H. Bé, and O. R. Anderson (1982), Effects of variations in light intensity on life processes of the planktonic foraminifer *Globigerinoides sacculifer* in laboratory culture, *J. Mar. Biol. Assoc. UK*, 62, 435–451.

Caron, D. A., W. W. Faber Jr., and A. W. H. Bé (1987), Growth of the spinose planktonic foraminifer *Orbulina universa* in laboratory culture and the effect of temperature on life processes, *J. Mar. Biol. Assoc. UK*, 67, 343–358.

Darling, K. F., C. M. Wade, I. A. Steward, D. Kroon, R. Dingle, and A. J. L. Brown (2000), Molecular evidence for genetic mixing of Arctic and Antarctic subpolar populations of planktonic foraminifera, *Nature*, 405, 43–47.

de Vargas, C., R. Norris, L. Zaninetti, S. W. Gibb, and J. Pawlowski (1999), Molecular evidence of cryptic speciation in planktonic foraminifers and their relation to oceanic provinces, *Proc. Natl. Acad. Sci.*, 96, 2864–2868.

de Vargas, C., S. Renaud, H. Hilbecht, and J. Pawlowski (2001), Pleistocene adaptive radiation in *Globorotalia truncatulinoides*: Genetic, morphologic, and environmental evidence, *Paleobiology*, 27, 104–125.

Di Lorenzo, E., A. J. Miller, N. Schneider, and J. C. McWilliams (2004), The warming of the California Current: Dynamics, thermodynamics and ecosystem implications, *J. Phys. Oceanogr.*, in press.

Duplessy, J. C., P. L. Blanc, and A. W. H. Bé (1981), Oxygen-18 enrichment of planktonic foraminifera due to gametogenic calcification below the euphotic zone, *Science*, 213, 1247–1249.

Emiliani, C. (1954), Depth habitats of some species of pelagic foraminifera as indicated by oxygen isotope ratios, *Am. J. Sci.*, 252, 149–158.

Fairbanks, R. G., and P. H. Wiebe (1980), Foraminifera and chlorophyll maximum: Vertical distribution, seasonal succession, and paleoceanographic significance, *Science*, 209, 1524–1526.

Fairbanks, R. G., M. Sverdlove, R. Free, P. H. Wiebe, and A. W. H. Bé (1982), Vertical distribution and isotopic fractionation of living planktonic foraminifera from the Panama Basin, *Nature*, 298, 841–844.

Field, D. B., and T. R. Baumgartner (2000), A 900 year stable isotope record of interdecadal and centennial change from the California Current, *Paleoceanography*, 15, 695–708.

Friddell, J. E., R. C. Thunell, and L. E. Heusser (2002), Direct comparison of marine and terrestrial climate variability during marine isotope stages 6 and 5: Results from Santa Barbara Basin ODP Hole 893A, *Paleoceanography*, 17(1), 1002, doi:10.1029/2000PA000594.

Friddell, J. E., R. C. Thunell, T. P. Guilderson, and M. Kashgarian (2003), Increased northeast Pacific climatic variability during the warm middle Holocene, *Geophys. Res. Lett.*, 30(11), 1560, doi:10.1029/2002GL016834.

Gastrich, M. D., and R. Bartha (1988), Primary productivity in the planktonic foraminifer *Globigerinoides ruber*, *J. Foraminiferal Res.*, 18, 137–142.

Hayward, T. L., and E. L. Venrick (1998), Nearsurface pattern in the California Current: Coupling between physical and biological structure, *Deep Sea Res. Part II*, 45, 1617–1638.

Hemleben, C., M. Spindler, and O. R. Anderson (Eds.) (1989), *Modern Planktonic Foraminifera*, 363 pp., Springer-Verlag, New York.

Hendershott, M. C., and C. D. Winant (1996), Surface circulation in the Santa Barbara Channel, *Oceanography*, 9, 114–121.

Hendy, I. L., and J. P. Kennett (1999), Latest Quaternary North Pacific surface-water responses imply atmosphere-driven climate instability, *Geology*, 27, 291–294.

Itou, M., T. Ono, T. Oba, and S. Noriki (2001), Isotopic composition and morphology of living *Globorotalia scitula*: A new proxy of sub-intermediate ocean carbonate chemistry?, *Mar. Micropaleontol.*, 42, 189–210.

Kincaid, E., R. C. Thunell, J. Le, C. B. Lange, A. L. Weinheimer, and F. M. H. Reid (2000), Planktonic foraminiferal fluxes in the Santa Barbara Basin: response to seasonal and interannual hydrographic changes, *Deep Sea Res. Part II*, 47, 1157–1176.

Lynn, R. J., and J. J. Simpson (1978), The California Current System: The seasonal variability

of its physical characteristics, *J. Geophys. Res.*, *92*, 12,947–12,966.

Miller, A. J. (1996), Recent advances in California Current modeling: Decadal and interannual thermocline variations, *Calif. Coop. Oceanic Fish. Invest.*, *37*, 69–80.

Mortyn, P. G., and C. D. Charles (2003), Planktonic foraminiferal depth habitat δ¹⁸O calibrations: Plankton tow results from the Atlantic sector of the Southern Ocean, *Paleoceanography*, *18*(2), 1037, doi:10.1029/2001PA000637.

Mulitza, S., A. Durkoop, W. Hale, G. Wefer, and H. S. Niebler (1997), Planktonic foraminifera as recorders of past surface-water stratification, *Geology*, *25*, 335–338.

Norton, J. G., and D. R. McLain (1994), Diagnostic patterns of seasonal and interannual temperature variation off the west coast of the United States: Local and remote large-scale atmospheric forcing, *J. Geophys. Res.*, *99*(C8), 16,019–16,030.

Oberhänsli, H., C. Bénier, G. Meinecke, H. Schmidt, R. Schneider, and G. Wefer (1992), Planktonic foraminifers as tracers of oceanic currents in the eastern south Atlantic, *Paleoceanography*, *7*, 607–632.

Ortiz, J. D., A. C. Mix, and R. W. Collier (1995), Environmental control of living symbiotic and asymbiotic foraminifera of the California Current, *Paleoceanography*, *10*, 987–1009.

Ortiz, J. D., A. C. Mix, W. Rugh, J. M. Watkins, and R. W. Collier (1996), Deep-dwelling planktonic foraminifera of the northeastern Pacific Ocean reveal environmental control of oxygen and carbon isotopic disequilibria, *Geochim. Cosmochim. Acta*, *60*, 4523–4590.

Pak, D. K., and J. P. Kennett (2002), A foraminiferal isotopic proxy for upper water mass stratification, *J. Foraminiferal Res.*, *32*(3), 319–327.

Patrick, A., and R. C. Thunell (1997), Tropical Pacific sea surface temperatures and upper water column thermal structure during the last glacial maximum, *Paleoceanography*, *12*, 649–657.

Peeters, F. J. C., and G.-J. A. Brummer (2002), The seasonal and vertical distribution of living planktic foraminifera in the NW Arabian Sea, in *The Tectonic and Climatic Evolution of the Arabian Sea Region*, edited by P. Clift et al., pp. 463–497, Geol. Soc., London.

Peeters, F. J. C., E. M. Evanova, S. M.-H. Conan, G. J. A. Brummer, G. M. Ganssen, S. R.

Troelstra, and J. E. Van Hinte (1999), A size analysis of planktic foraminifera from the Arabian Sea, *Mar. Micropaleontol.*, *36*, 31–63.

Pond, S., and G. L. Pickard (1991), *Introductory Dynamical Oceanography*, 2nd ed., 329 pp., Pergamon, New York.

Ravelo, A. C., and R. G. Fairbanks (1992), Oxygen isotopic composition of multiple species of planktonic foraminifera: Recorders of the modern photic zone temperature gradient, *Paleoceanography*, *7*, 815–831.

Roemmich, D. (1989), Mean transport of mass, heat, salt, and nutrients in southern California coastal waters: Implications for primary production and nutrient cycling, *Deep Sea Res.*, *36*, 1359–1378.

Roemmich, D., and J. McGowan (1995), Climatic warming and the decline of zooplankton in the California Current, *Science*, *267*, 1324–1326.

Sachs, K. N., R. Cifelli, and F. T. Bowen (1964), Ignition to concentrate shelled organisms in plankton samples, *Deep Sea Res.*, *11*, 621–622.

Sautter, L. R., and R. C. Thunell (1991a), Seasonal variability in the oxygen and carbon isotopic composition of planktonic foraminifera from an upwelling environment: sediment trap results from the San Pedro Basin, Southern California Bight, *Paleoceanography*, *6*, 307–334.

Sautter, L. R., and R. C. Thunell (1991b), Planktonic foraminiferal response to upwelling and seasonally variable hydrographic conditions: Sediment trap results from the San Pedro Basin, Southern California Bight, *J. Foraminiferal Res.*, *21*, 347–363.

Scripps Institution of Oceanography (SIO) (2002), Physical, chemical, and biological data: CalCOFI Cruises 0107 and 0110, *SIO Ref. 02–07*, La Jolla, Calif.

Shackleton, N. J., J. D. H. Wiseman, and H. A. Buckley (1973), Non-equilibrium isotopic fractionation between seawater and planktonic foraminiferal tests, *Nature*, *242*, 177–179.

Simpson, J. J. (1992), Response of the southern California current system to the mid-latitude North Pacific coastal warming events of 1982–1983 and 1940–1941, *Fish. Oceanogr.*, *1, 57–75*.

Spero, H. J. (1992), Do planktic foraminifera accurately record shifts in the carbon isotopic

composition of seawater ΣCO₂?, *Mar. Micropaleontol.*, *19*, 275–285.

Spero, H. J., and D. W. Lea (1996), Experimental determination of stable isotope variability in *Globigerina bulloides*: Implications for paleoceanographic reconstructions, *Mar. Micropaleontol.*, *28*, 231–246.

Spindler, M., C. H. Hemleben, J. B. Salomons, and L. P. Smit (1984), Feeding behavior of some planktonic foraminifers in laboratory cultures, *J. Foraminiferal Res.*, *14*(4), 237–249.

Stott, L. D., and C. M. Tang (1996), Reassessment of foraminiferal-based tropical sea surface δ¹⁸O paleotemperatures, *Paleoceanography*, *11*, 37–56.

Thunell, R. C., and L. Reynolds (1984), Sedimentation of planktonic foraminifera: Seasonal changes in species flux in the Panama Basin, *Micropaleontology*, *30*, 241–260.

Thunell, R. C., E. Tappa, C. Pride, and E. Kincaid (1999), Sea-surface temperature anomalies associated with the 1997–1998 El Niño recorded in the oxygen isotope composition of planktonic foraminifera, *Geology*, *27*, 843–846.

Vincent, E., and W. H. Berger (1981), Planktonic foraminifera and their use in paleoceanography, in *The Sea*, vol. 7, edited by C. Emiliani, pp. 1025–1119, John Wiley, Hoboken, N. J.

Watkins, J. M., and A. C. Mix (1998), Testing the effects of tropical temperature, productivity, and mixed-layer depth on foraminiferal transfer functions, *Paleoceanography*, *13*, 96–105.

Weinheimer, A. L., J. P. Kennett, and D. R. Cayan (1999), Recent increase in surface-water stability during warming off California as recorded in marine sediments, *Geology*, *27*, 1019–1022.

Wiebe, P. H., A. W. Morton, A. M. Bradley, R. H. Backus, J. E. Craddock, V. Barber, T. J. Cowles, and G. R. Flierl (1985), New developments in the MOCNESS, an apparatus for sampling zooplankton and micronekton, *Mar. Biol.*, *87*, 313–323.

———————————

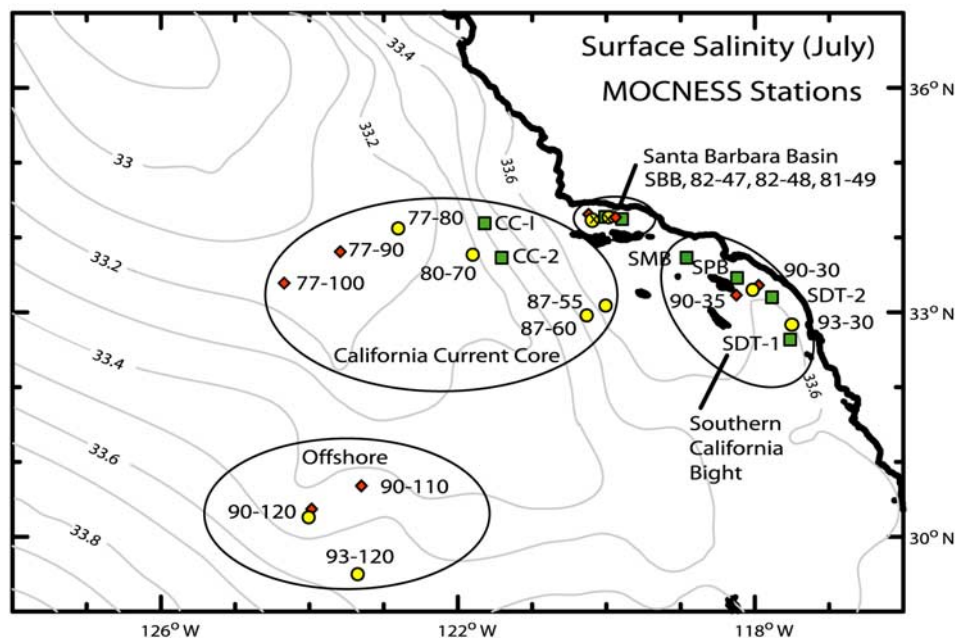D. B. Field, Scripps Institution of Oceanography, La Jolla, CA 92093, USA. (bgdave@uscd.edu)

Figure 1. Location of MOCNESS sampling stations overlain on average surface salinity (July) as an indictor of circulation in the CCS [after *Lynn and Simpson*, 1978]. Station locations are shown for spring cruise SP 0103 (square), summer cruise NH 0107 (diamond), winter cruise NH 0001 (cross), and winter cruise JD 0201 (circle). The different hydrographic regions are circled (Santa Barbara Basin, California Current Core, Southern California Bight, and offshore). Sampling details in Table 1.
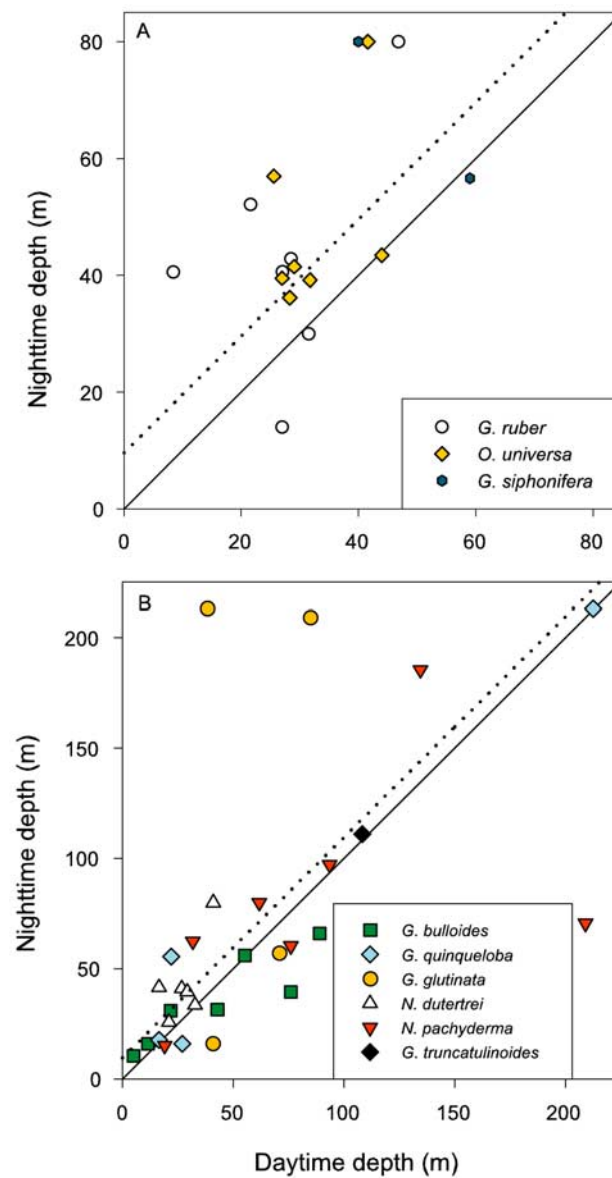
Figure 7. Comparison of the midpoint of day and night vertical distributions for (a) species with symbiotic algae and (b) the nonsymbiont (*G. bulloides*, *G. quinqueloba*, and *N. pachyderma*) and facultative symbiont-bearing species (*N. dutertrei*, *G. glutinata*, and *G. truncatulinoides*). Solid line shows the 1:1 relationship. Dotted line shows the average difference in pycnocline depth (10 m) between the day and night stations.
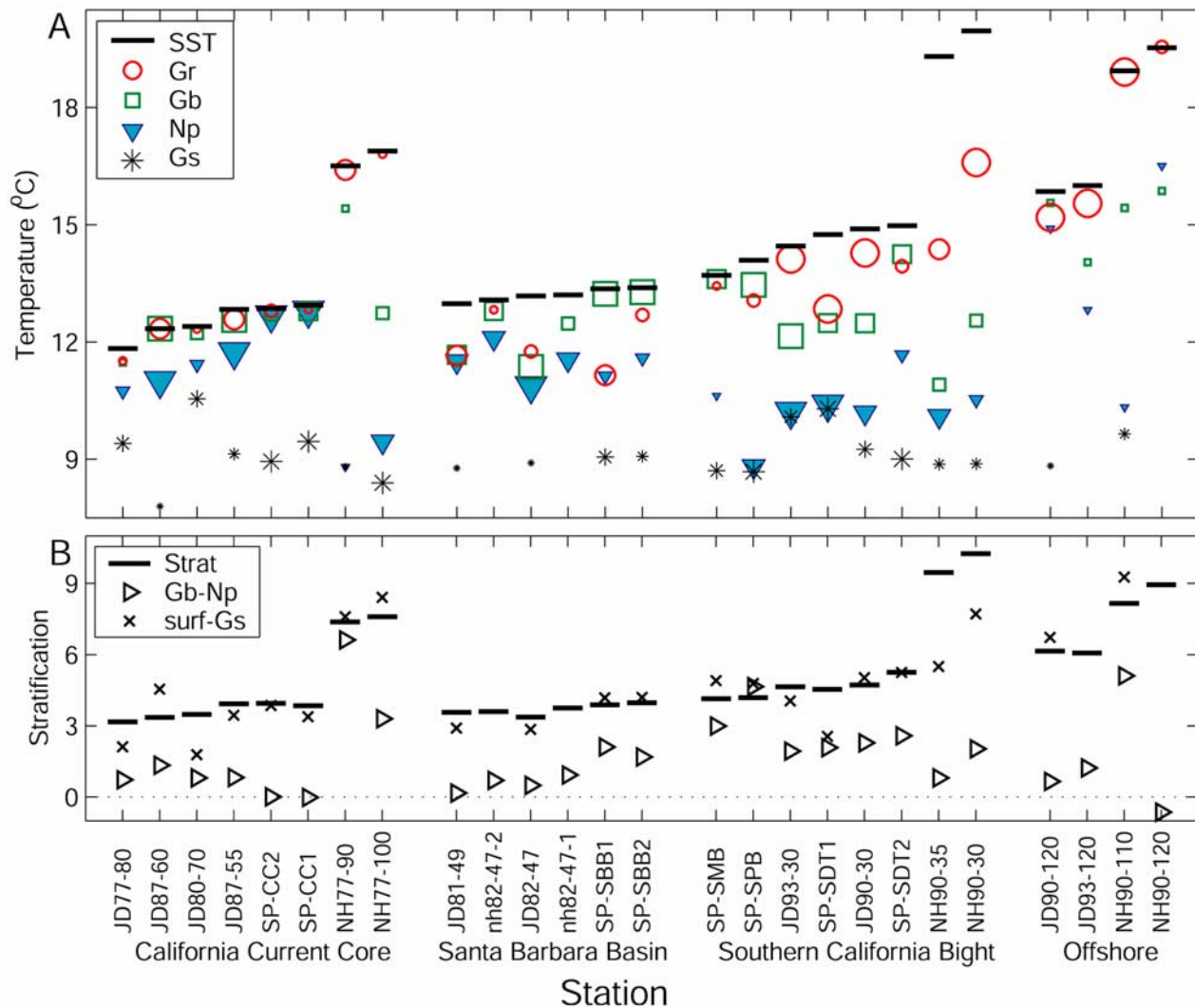
Figure 11. (a) Summary of measured SST and weighted mean temperature of the core 50% of four species of foraminifera indicating variability in temperature signatures by region and sampling station (*G. bulloides*, Gb; *G. rubber*, Gr; *N. pachyderma*, Np; and *G. scitula*, Gs). (b) Measured thermal stratification (0–150 m) and two foram-derived indices of stratification. The Gb-Np index is the difference between weighted mean temperature of *G. bulloides* and *N. pachyderma*. The surf-Gs index is the difference between whichever near surface dweller provides a higher temperature index (either *G. bulloides* or *G. ruber*) and *G. scitula*. Sizes of symbols in Figure 11a are proportional to quartiles of abundance as in Figure 8. Winter stations are JD and nh. Summer stations are NH. Spring stations are SP.
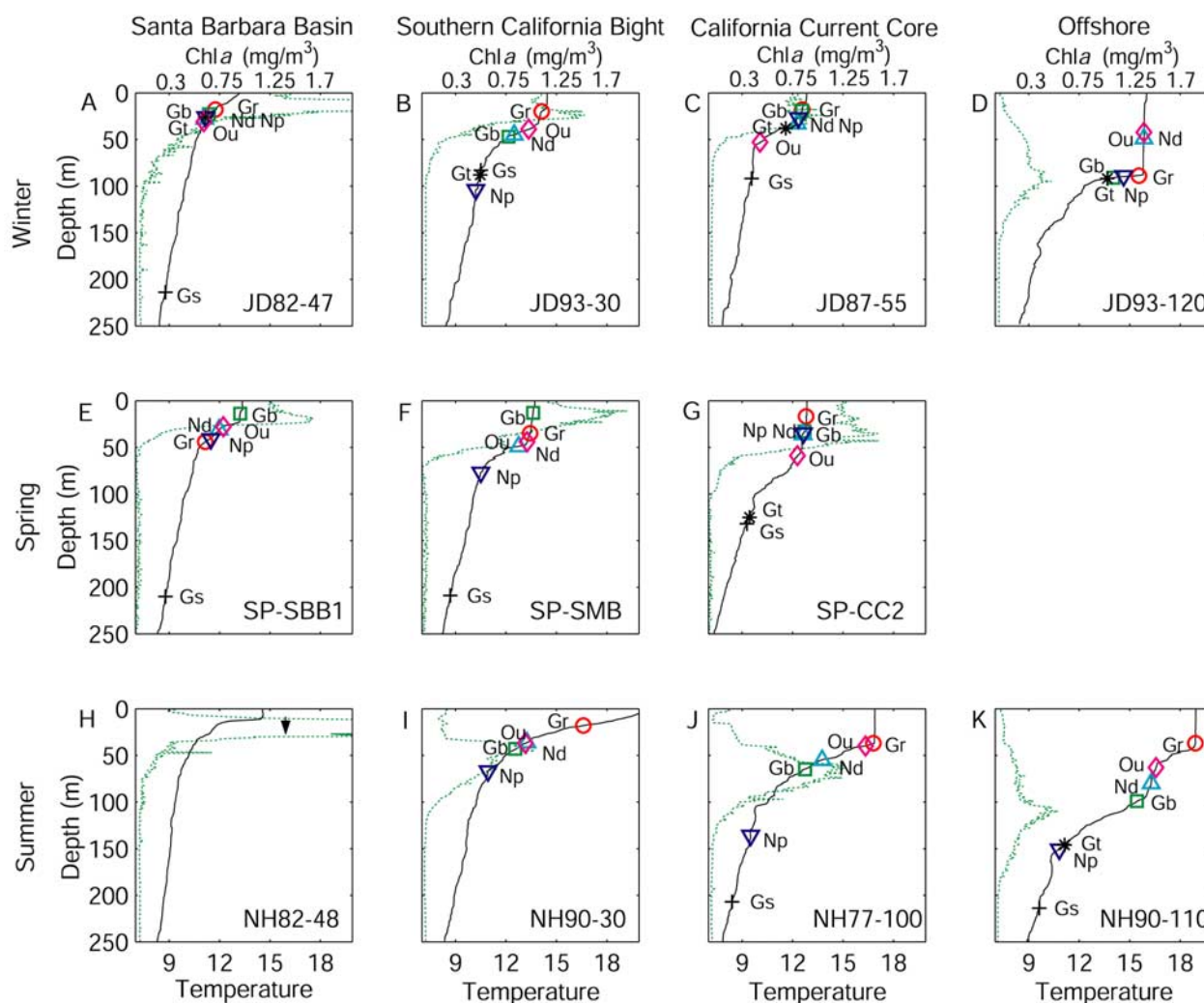
Figure 12. Variability of habitat depth and associated temperature (solid line) and chlorophyll *a* (dotted line) of the core 50% of the population for the principal species of this study (*G. bulloides*, Gb; *G. rubber*, Gr; *O. universa*, Ou; *N. dutertrei*, Nd; *N. pachyderma*, Np; *G. truncatulinoides*, Gt; and *G. scitula*, Gs). One representative station is illustrated for each hydrographic region and season. The offshore region was not sampled during spring. Arrow at the SBB station in summer indicates that each foraminiferal species was more abundant within or beneath the chlorophyll maximum than in the mixed layer.
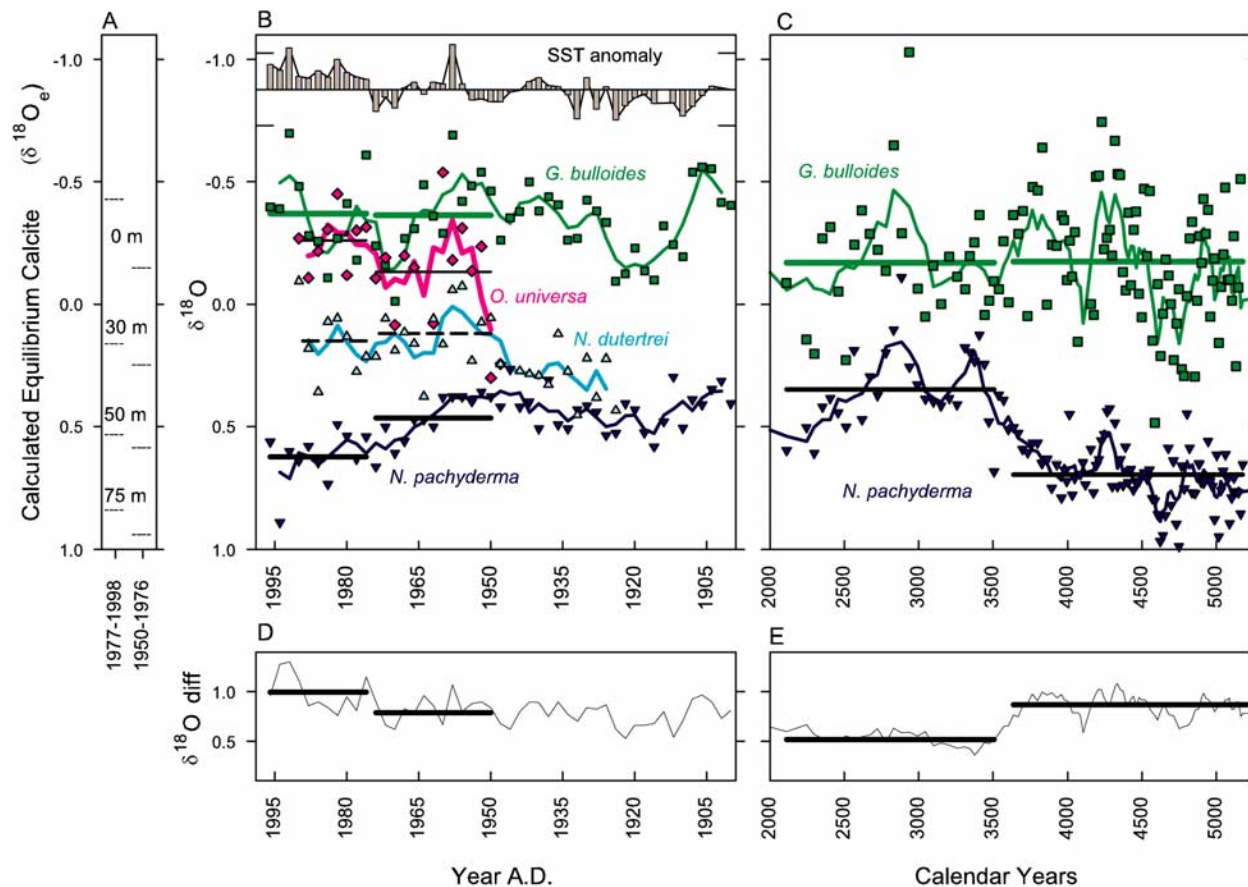
Figure 13. Comparison of downcore isotopic records from the Santa Barbara Basin (SBB) sediments and hydrographic measurements illustrating different time intervals where changes in foraminifera $\delta^{18}O$ depart from expectations for a single depth. (a) Calculated equilibrium calcite values ($\delta^{18}O_e$) at several depths from CalCOFI hydrographic data for the periods 1949–1976 and 1977–1998 [*Field and Baumgartner*, 2000]. (b) The 20th century $\delta^{18}O$ records of *G. bulloides* and *N. pachyderma* in 2-year intervals from *Weinheimer et al.* [1999], together with measurements from *N. dutertrei* and *O. universa* (Field et al., unpublished data, 2002) using the approach described in the work of *Field and Baumgartner* [2000] but using 2-year intervals. Also shown in Figure 13b are normalized SST anomalies from Comprehensive Ocean-Atmospheric Data Set (COADS) data off the west coast of North America, extending from Canada to northern Baja California. (c) The mid-Holocene record from *Friddell et al.* [2003] with measurements every 13–52 years (from 5200 to 2000 years before present). In Figures 13b and 13c varying lines show three point running averages for clarity. Horizontal bars are the average values of all measurements within a selected time interval. Ordinate axis is inverted in Figures 13a–13c to be consistent with changes in temperature. The lower $\delta^{18}O_e$ values at fixed depths over the SBB in 1977–1998 relative to 1950–1976 are not observed in the records of *G. bulloides*, *N. pachyderma*, or *N. dutertrei*. (d) Stratification index and (e) from the difference in each $\delta^{18}O$ value between *G. bulloides* and *N. pachyderma* (thin line) and the average of the index for each chosen period (bold horizontal bar).