Seasonality and depth distribution of a mesopelagic foraminifer, *Hastigerinella digitata*, in Monterey Bay, California

Pincelli M. Hull,[a,1,*] Karen J. Osborn,[a,b] Richard D. Norris,[a] and Bruce H. Robison[c]

[a] Scripps Institution of Oceanography, University of California, San Diego, La Jolla, California
[b] University of California, Santa Cruz, Institute of Marine Sciences, Santa Cruz, California
[c] Monterey Bay Aquarium Research Institute, Moss Landing, California

Abstract

We investigated the habitat depth and population dynamics of mesopelagic foraminifera in Monterey Bay, California, using 12 yr of video surveys and specimens from live collections. The water column over Monterey Canyon continuously supports two distinct species of mesopelagic foraminifera, *Hastigerinella digitata* and a previously unknown species referred to as *Hastigerina* sp., with *H. digitata* dominating the planktonic foraminiferal assemblage at mesopelagic depths. *H. digitata* populations live within a narrow depth horizon that lies above the core of the regional oxygen minimum zone at a depth of 280–358 m and O_2 concentrations of 1–1.3 mL L^{-1}. Our observations provide a modern calibration for understanding fossil digitate planktonic foraminifera. We observed numerous copepods in various stages of ingestion on the spines of *H. digitata* and a conspicuous lack of detritus attached to the spine network, providing support for the hypothesis that *H. digitata* is an obligate carnivore. *H. digitata* populations did not show the strong two-phase seasonality that characterizes the population dynamics of many mesopelagic species that live above the Monterey Canyon, although *H. digitata* was generally more abundant in cooler waters on seasonal and interannual timescales.

The ecology of midwater organisms—inhabitants of the waters lying below the well-lit surface waters and above the deep seafloor—is poorly known despite the areal extent of their habitat and their long evolutionary history (Robison 2004, 2009). The lack of information pertaining to the largest ecosystem on Earth (by volume) arises in part from the difficulty of accessing the midwater habitat and limitations of studying communities with trawl nets and acoustics. Trawl nets destroy the delicate organisms that make up a major component of midwater communities and preclude observations of organism interactions in situ. Acoustics generally cannot provide count data or distinguish between individuals and/or species (NRC 2003; Robison 2004). The advent of remotely operated vehicle (ROV) technology provided a needed complement to trawl and acoustic sampling by allowing the direct observation of organismal behavior in nature (Haddock 2007) and by enabling the collection of time series of the relative abundance and depth distribution of taxa (Robison et al. 1998; Robison 2004; Osborn et al. 2007).

Here, we investigate the ecology and distribution of mesopelagic planktonic foraminifera in Monterey Bay, California, using 12 yr of effort-standardized, ROV video transect observations and specimens captured in situ with a ROV. We focus on planktonic foraminifera, just one of the many mesopelagic groups quantified within the ROV time series, as they showcase the potential of ROV video transects to provide reliable, in situ observations of even small organisms that were poorly sampled and understood with traditional plankton net sampling. As such, this study provides baseline data on the population dynamics and distribution of mesopelagic foraminifera and serves as a benchmark for future studies of mesopelagic populations.

Planktonic foraminifera are marine protists that are distributed globally in oceanic surface waters. Species with mesopelagic depth distributions are known from contemporary plankton tows and have been inferred on the basis of morphology and geochemistry in the fossil record (Coxall et al. 2007). Most species of modern foraminifera are primarily epipelagic, although some descend into mesopelagic waters for reproduction or seasonal survival (Fairbanks et al. 1982; Hemleben et al. 1989). Modern species with primarily or entirely mesopelagic depth distributions commonly possess digitate chambers (Hemleben et al. 1989; Coxall et al. 2007). Digitate chambers, defined by the presence of one or more fingerlike extensions from chambers in the final whorl (Fig. 1A,C–G; *see* operationalized definition in Coxall et al. [2007]), are not observed in extant epipelagic species. There are three living digitate species, *Hastigerinella digitata* (Rhumbler 1911), *Globigerinella adamsi* (Banner and Blow 1959), and *Beella digitata* (Brady 1879); all are generally known from low to mid latitudes worldwide (Bé 1977; Coxall et al. 2007). Oblique plankton tows and depth-stratified tows indicate that extant digitate species occur primarily in the water column below 200 m in depth (Rhumbler 1911; Bradshaw 1959; Bé 1977) and comprise a rare component of both planktonic and fossil assemblages (Prell et al. 1999; Coxall et al. 2007).

H. digitata, G. adamsi, and *B. digitata* are all equipped with a dense spine network believed to represent a functional adaptation for capturing active prey (Hemleben et al. 1989). Planktonic foraminifera with spines are able to successfully capture and consume living zooplankton in captive feeding experiments, whereas most non-spinose

---

* Corresponding author: pincelli.hull@yale.edu

[1] Present address: Yale University, Department of Geology and Geophysics, New Haven, Connecticut
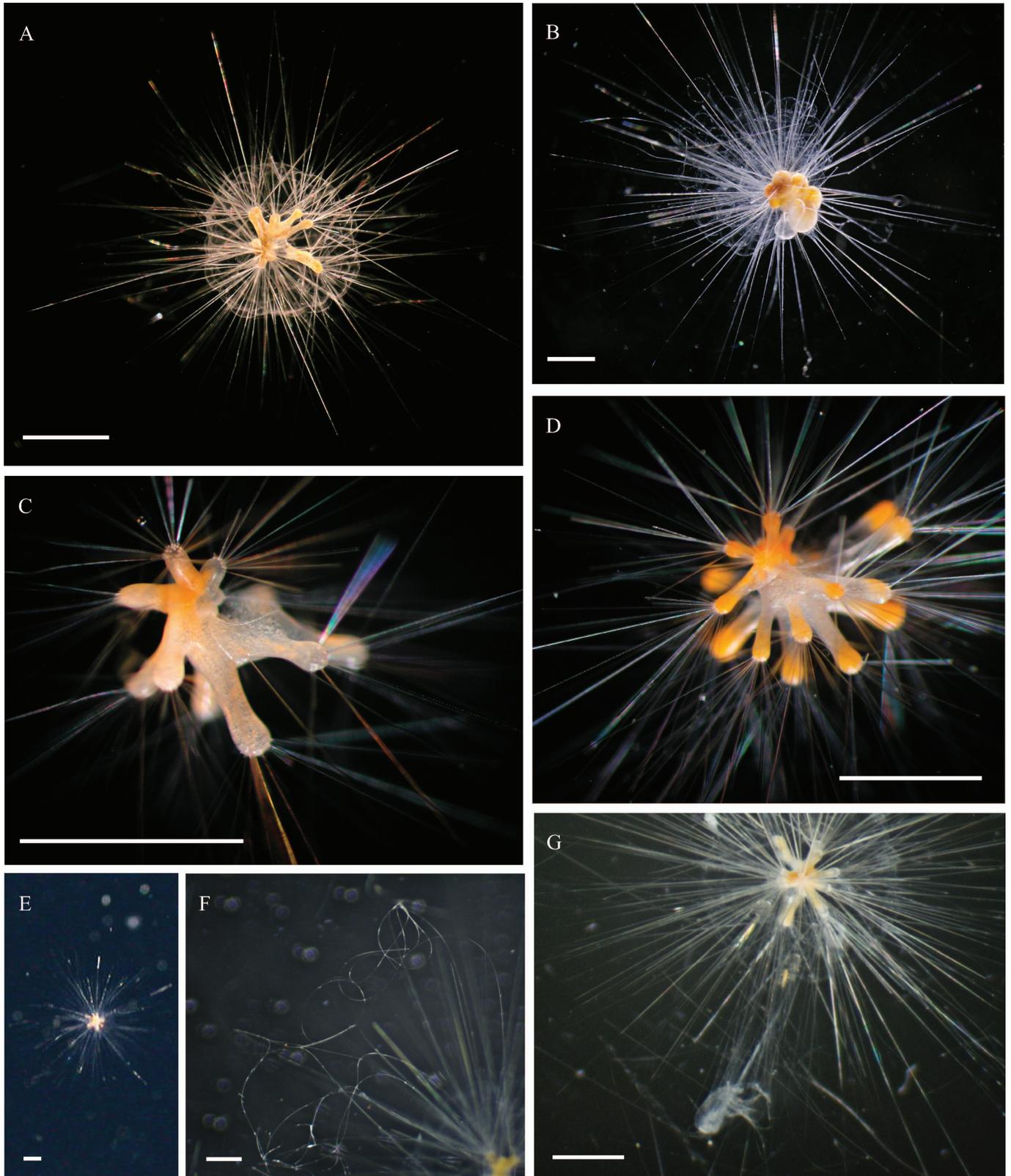
Fig. 1.   Light microscopic and video images of (A, C–G) *Hastigerinella digitata* and (B) *Hastigerina* sp. Bubble capsules are seen in A, B, and E–G. The specimen in (C) is at an early ontogenetic stage, while the specimen in (D) is inferred to be at the maximum size and to have the maximum number of digitate projections on the final chamber (four). (E) Video frame-grab of an individual in situ taken with the ROV. (F) Extension of the rhizopodia off the ends of an individual's spines; note the tangling of rhizopodia that occurs during handling. (G) Typical sized copepod, freshly captured and covered with numerous rhizopodia. All scale bars (white) are 2 mm.

species cannot (Bé et al. 1977; Spindler et al. 1984). *H. digitata* is thought to be strictly carnivorous, while *G. adamsi* and *B. digitata* may be relatively more omnivorous (C. Hemleben pers. comm., as cited in Coxall et al. [2007]). No selective advantage in maintaining buoyancy has been demonstrated for spines, although it has been hypothesized (Lipps 1979), and living planktonic foraminifera maintain notably stable depth distributions in spite of negatively buoyant tests (Hemleben et al. 1989).

Digitate planktonic foraminifera have a rich fossil record, beginning 130 million yr ago in the early Cretaceous. Stable isotope studies indicate that most fossil digitate species lived in deep-water habitats below the thermocline and are hypothesized to have lived near or in oxygen minimum zones (Coxall et al. 2007). The current interpretation of fossil digitate planktonic foraminifera is limited in part by a lack of detailed information on the biology and ecology of living representatives. Thus, our study provides new, highly resolved records of one modern digitate foraminifera, *H. digitata*, that can be used to further calibrate and interpret the fossil record. Digitate morphologies have evolved in many lineages since the early Cretaceous, indicating widespread convergent morphological and ecological evolution of mesopelagic species (Coxall et al. 2007). Morphological and ecological convergence is common in planktonic foraminifera, with the convergent evolution of similar basic body plans multiple times in the fossil record (iterative evolution; Cifelli 1969; Norris 1991) and with the polyphyletic origination of planktonic foraminifera from benthic ancestors (Darling et al. 1997; de Vargas et al. 1997; Longet and Pawlowski 2007).

We describe in situ observations and surveys of the ecology and distribution of two mesopelagic foraminifera in Monterey Bay, California—*H. digitata* and a new midwater species, *Hastigerina* sp.—using a 12-yr, depth-stratified, video time-series survey and live collections as part of the Midwater Ecology Program at the Monterey Bay Aquarium Research Institute (MBARI). The closest known relative of *H. digitata* and *Hastigerina* sp. is the tropical, shallow-dwelling *Hastigerina pelagica*, for which relatively detailed ecological and life-history observations are available (Anderson and Be 1976; Spindler et al. 1979; Loncaric et al. 2005). In our analysis of *H. digitata* and *Hastigerina* sp. we compare our ROV observations and inferences with known ecological characteristics of *H. pelagica* and also consider the phylogenetic affinities of the morphologically similar *Hastigerina* sp. and *H. pelagica*.

Our mesopelagic observations in Monterey Bay comprise the longest high-resolution, quantitative time series of mesopelagic fauna reported to date and the first long-term high-resolution in situ study of planktonic foraminifera. We find that *H. digitata* populations have a remarkably narrow and stable depth distribution, with weak seasonality and environmental correlates of standing abundance, providing new insight into the structure and stability of pelagic communities found between 100 m and 1000 m in depth. Both findings are surprising given the environmental variation in the water column of Monterey Canyon and patterns found in other mesopelagic organisms (Silguero and Robison 2000; Raskoff 2001), and this unusual

consistency may be influenced by several mechanisms. We also report observations on the trophic ecology and morphology of *H. digitata* and *Hastigerina* sp.

Methods

Study site—Our study is based upon a series of quantitative ROV video surveys made in Monterey Bay at a single location over the axis of the Monterey Submarine Canyon (36°42′N, 122°02′W; water column depth 1600 m). Seafloor depth increases rapidly to the west, such that the area is open to oceanic water. Monterey Bay is part of the greater California Current System, which consists of subarctic surface water moving from north to south along the coast from southern British Columbia to Baja California. The California Current typically extends from the surface to approximately 300 m in depth and is slow moving and characterized more by eddies and offshore jets than by uniform flow (Lynn and Simpson 1987). The California Undercurrent runs year-round, below and counter to the California Current (Chelton 1984; Collins et al. 2003). The Davidson Current runs seasonally northward at the surface, inshore of the California Current. Two distinct seasons are recognized in Monterey Bay with regard to salinity, oxygen, and nutrients: the upwelling and non-upwelling seasons (Silguero and Robison 2000). The upwelling occurs roughly between April and November and is characterized by a shallow thermocline, high nutrients, and high primary production (Olivieri and Chavez 2000; Silguero and Robison 2000). Our study site is located 7.3 km south of MBARI's hydrographic Sta. M 1, where time-series data in the upper water column show long-term consistency with seasonal patterns and conditions in the California Current off central California (Pennington and Chavez 2000).

Midwater time series—We examined the depth distribution and temporal abundance patterns of *H. digitata* using annotated video transects and transits from the MBARI video archives. Video transects refer to a quantitative time series conducted by the Midwater Ecology Program at MBARI, which consists of standardized monthly video transects made at discrete depth increments (10-min transects at 100-m intervals between 100 and 1000 m). During transects, the ROV was driven at a constant speed (measured in real time by an acoustic current meter) for 10 min, with the camera at a fixed setting. Transects typically covered a horizontal distance of 350 m and recorded the contents of an average volume of 1400 ± 225 m³ of water (Robison et al. 1998; Robison et al. 2005). The heading taken by the ROV during transects was determined by winds at the surface and by currents below. In contrast, video transit data included annotated observations made while the ROV was transiting from one depth interval to the next and during exploratory ROV use on Midwater Ecology dives. Unlike the video transects, transit observations for this study were not standardized by the amount of time spent at depth or to the ROV orientation, driving speed, or camera settings. We refer to video transect and video transit data as transect$_{quantitative}$
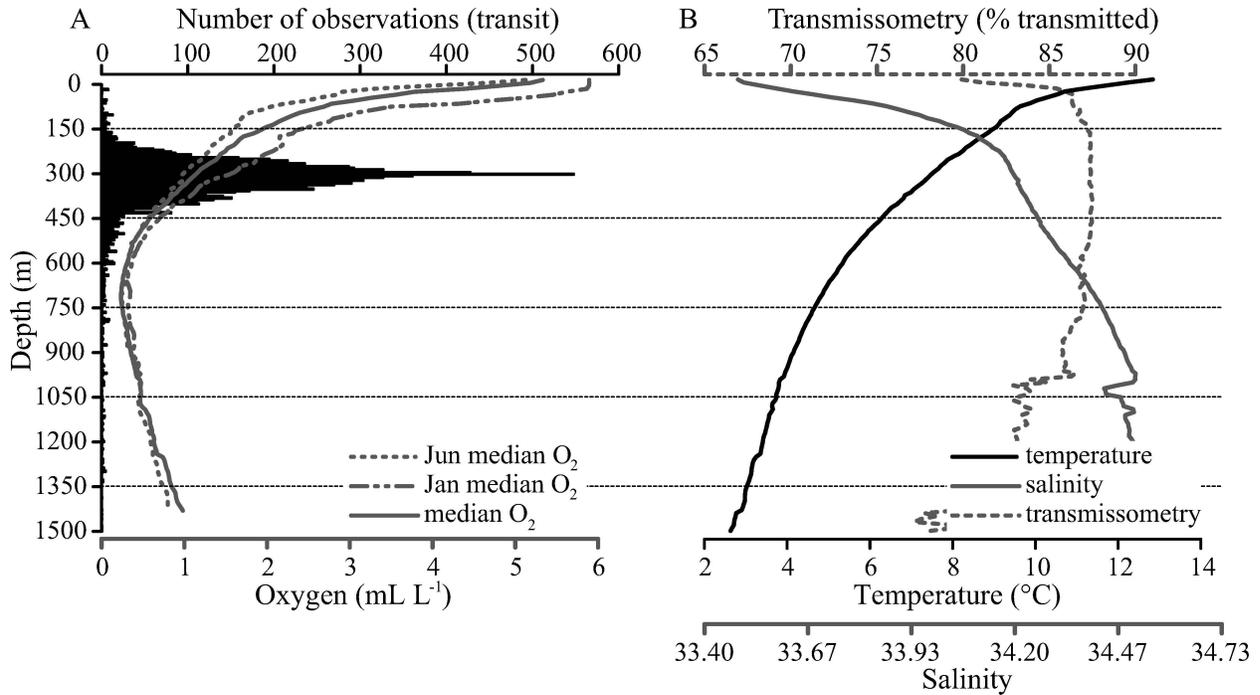
Fig. 2. Depth of all transit$_{non-standardized}$ observations of *Hastigerinella digitata* over the Monterey Canyon between 2002 and 2008. (A) Median dissolved oxygen (mL L^{-1}) is shown for 10-m depth bins across all transit observations between 2002 and 2008 (solid line), with the median June dissolved oxygen (dotted line) and the median January dissolved oxygen (dashed line). Total transit$_{non-standardized}$ observations for a 10-m depth bin are plotted. (B) Median temperature (black line), salinity (gray line), and percent transmittance (dotted line) are shown for 10-m depth bins across all observations between 2002 and 2008.

and transit$_{non-standardized}$, respectively, to avoid confusion due to the similarity of the terms 'transect' and 'transit.' Temperature, salinity, and depth were measured continuously on all dives with a Sea-Bird SBE-9 mounted on the ROV and linked to video observations by the video time code. Oxygen concentration was measured with a Sea-Bird SBE-43 and particle density with a Sea Tech 25-cm transmissometer. We used these conductivity temperature–depth (CTD)–based measurements, binned into 10-m depth increments, for all analyses of environmental correlates.

Video surveys were annotated after each dive by specialist technicians at MBARI. The spines and rhizopods of *H. digitata* sparkle under the ROV's lights and create a distinctive video signature (Fig. 1E); video observations were confirmed to be *H. digitata* by directed High-Definition (HD) imaging and live captures by the ROV in September 2008, November and December 2009, and March 2010. We interpret all video observations as living *H. digitata,* as we failed to collect any empty shells in the live ROV captures and because we suspect that dead shells would have a different video signature due the passive accumulation of marine snow, a lack of rhizopodial extensions, and the rapid dissolution of spines upon death (as observed in collected specimens). Exceptional occurrences of *H. digitata* (occurrences recorded below 1000 m and in months with exceptionally high or low counts) and 56 previously unannotated transects were annotated by the authors (K.J.O., R.D.N., and P.M.H.) for this study. The accuracy and repeatability of *H. digitata* annotations were

checked by K.J.O., R.D.N., and P.M.H. by repeating a transect annotation; *H. digitata* counts were replicated within plus or minus three observations. We note that only the very largest *H. digitata* are visible from the midwater transect tapes because of the speed of the vehicle. When the ROV stopped moving, we could see additional, smaller foraminifera, including both small *H. digitata* and *Hastigerina* sp., as confirmed by collections. Therefore, the abundances we report here from video data apply only to the largest size class of *H. digitata* and not to the total abundance of mesopelagic foraminifera over the Monterey Canyon. Single-chamber stable isotope analyses are planned to test for ontogenetic variation in the habitat depth of *H. digitata* in future research.

We quantified the long-term and seasonal depth distribution of *H. digitata* primarily using video transits$_{non-standardized}$. Transit$_{non-standardized}$ observations provide a continuous picture of the depth distribution of *H. digitata* but are subject to bias introduced by the lack of normalization to the time spent at each depth. However, we found that the long-term, non-standardized depth distribution data for *H. digitata* (Fig. 2A) accurately reflect the distribution data recorded from transects$_{quantitative}$. Additionally, the seasonal changes we report in depth distributions from transit$_{non-standardized}$ data were too narrow to have been caused by sampling bias alone. Midwater explorations are typically focused at 100-m intervals, whereas the transit data revealed a finer-scale vertical structure in foraminifer population densities. Depth distribution data were only considered from the period between

2002 and 2008 (9614 transit$_{non-standardized}$ observations), as these represent well-annotated years (i.e., years with more than 500 observations yr^{-1}), in contrast to data from before 2002, when sparser records might be more susceptible to sampling-effort biases.

We considered the population dynamics of *H. digitata* using midwater transect$_{quantitative}$ data between 1997 and 2008 at the depth of peak *H. digitata* abundance (300 m, 4606 *H. digitata* observations from 1997 to 2008). By restricting our study of population dynamics to a single depth interval, we were able to annotate all missing transects$_{quantitative}$ and to check transects with unusually high or low abundances. We primarily used annotations from HD tapes, although before October 1999 and for 11 scattered months between October 1999 and November 2008 only BetaCam tapes were available. A comparison of records annotated for both BetaCam and HD tapes from the same transects revealed no significant bias between the two recording types with regard to the target species.

Live collections—Live collections of planktonic foraminifera were made on 16 September 2008, 17 November 2009, 03 December 2009, and 15 and 18 March 2010. Live specimens were collected using both a high-flow suction sampler and detritus samplers on ROV *Ventana* (Robison 1992). In many cases individuals were observed to still have extended rhizopodia and intact bubble networks (Fig. 1) when the ROV returned to the deck of the ship. Specimens were transferred to the laboratory ashore, where they were observed, measured, and photographed using a Nikon SMZ-U dissecting microscope and attached Nikon Coolpix 5000.

Environmental variables—We examined 11 environmental variables as potential determinants of *H. digitata* abundance and depth distribution. Temperature, salinity, depth, oxygen concentration, and particle density were measured directly from the ROV and were considered at three depths: (1) the surface (10 m), (2) the approximate thermocline (60 m), and (3) at the depth of peak *H. digitata* abundance (300 m). Particle density was only considered at 300 m and was interpreted as an indicator of export production to this depth (Bishop 1999). Three environmental variables were derived from the instrument data: density, stratification, and spiciness. Density was calculated from temperature, salinity, and depth. A stratification index was calculated as the 10–300-m density difference. Spiciness, a temperature and salinity metric useful in the identification of water masses (Flament 2002), was calculated using updated code and algorithms provided by B. Schlining (Schlining 1999). The other three variables— upwelling, North Pacific Oscillation Index (NOI, a regional El Niño–Southern Oscillation index), and the North Pacific Gyre Oscillation (NPGO, a decadal climatic oscillation [Di Lorenzo et al. 2008])—are regional indices and were obtained from the National Oceanic and Atmospheric Administration (http://www.pfeg.noaa.gov/products/) and the NPGO website (http://eros.eas.gatech.edu/npgo/). We used the upwelling anomaly recorded from the closest available buoy (MBARI's M 1 at 36°N, 122°W).

Statistical analysis—Seasonal trends in depth distributions and abundance were assessed using median monthly depth (transit$_{non-standardized}$ data) and median monthly abundance at 300 m (transect$_{quantitative}$ data). A pairwise Wilcoxon rank sum test with a Bonferroni correction for multiple comparisons was used to test for differences between months. Spearman's rank correlation ρ was then used to test for environmental correlates of median monthly depth and abundance. Finally, we used Pearson's correlation coefficient to test individual correlates of *H. digitata* abundance at 300 m for the entire time series using monthly data (115 months over the course of 12 yr).

We tested whether changes in *H. digitata* populations at 300-m depth were significantly different from random variations using a runs test for randomness. This test was important, as we might expect *H. digitata* abundance at 300 m to vary randomly for a number of reasons unrelated to the changes in the standing abundance, including the spatial and temporal patchiness of plankton populations on scales not quantified within this time series or annotation error due to the small size of *H. digitata*. We rejected the null hypotheses of a random time series using a two-tailed runs test ($p = 0.023$) on the sign (increasing or decreasing) of the change in population abundance between successive months. Subsequent one-tailed runs tests indicated that the abundance of *H. digitata* varies more than would be expected by random chance ($p = 0.011$). Our conclusions were unchanged by how we handled missing months (29 missing out of a 144-month series), including ignoring months bordering gaps or assuming median, same-sign, or opposite-sign changes for missing months.

We also investigated the underlying dynamics of the time-series data for *H. digitata* abundance, testing for linear stochastic vs. non-linear population dynamics, as has been reported in other populations in the California Current (Hsieh et al. 2005*a,b*; Hsieh and Ohman 2006). To this end, we used multiple methods, including time-lag plots and time-residual plots (Sugihara et al. 1999), and simplex projection with S-mapping (simplex-projection analyses by H. Ye, after the method of Hsieh et al. [2005*a*]). Gaps within the time series restricted our tests to non-linear dimensionalities of 1–4, and the time-series length reduced the power of the S-mapping approach (Hsieh et al. 2008). However, within this limited scope, linear predictions performed as well as non-linear predictions (H. Ye, results not shown), supporting the use of the linear methods detailed above.

Results

Species present—We collected live specimens of two species of planktonic foraminifera at depths from 213 to 378 m (Fig. 1). The most abundant species in our collections, *H. digitata* (42 individuals captured), is characterized by a spine network anchored on the terminations of large digitate chambers (Fig. 3) and a bubble network suspended from the spines and encapsulating the test (Fig. 1). The second species, which we refer to as *Hastigerina* sp. (14 individuals captured), broadly resembles *H. digitata* but is typically smaller than *H.*
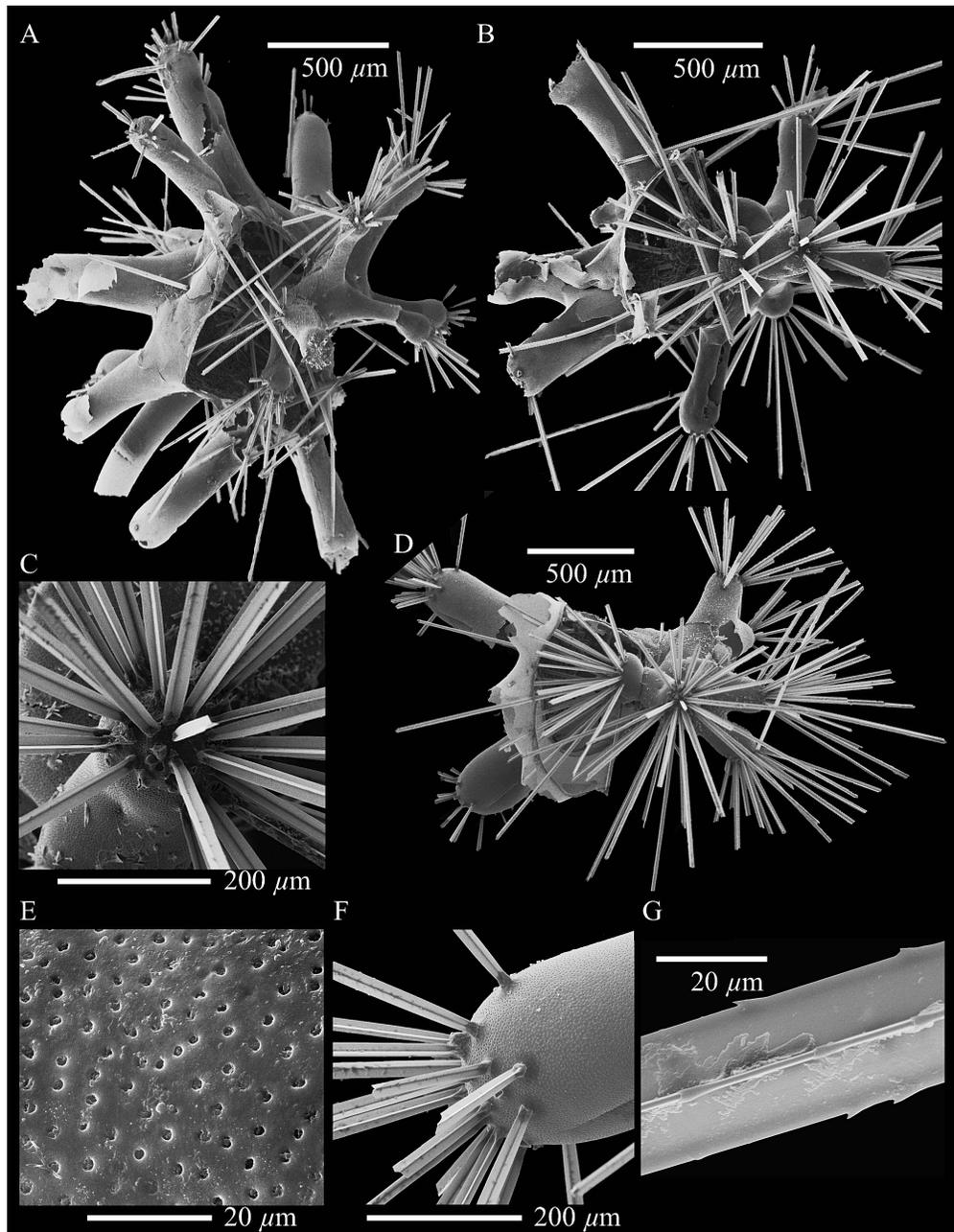
Fig. 3. Scanning electron microscope (SEM) images of (A, B, D) *Hastigerinella digitata* showing the serial addition of chambers through ontogeny, with (A) representing a later stage and (D) an earlier stage adult, respectively. (A, B) Characteristic streptospiral coiling of *H. digitata*. (C–F) Spine density, shape, and base shape, with (G) fine spine teeth illustrated. All spines are broken at the approximate point of contact with the edge of the bubble capsule; heavy damage to test walls in all images was incurred in preparing specimens for SEM. (E) Typical wall structure.

digitata, lacks digitate extensions on chambers (1–4 extensions are found in *H. digitata*), has a more even distribution of triradiate spines, and has planispiral rather than streptospiral coiling (Fig. 4).

We think it unlikely that *Hastigerina* sp. is a large, deep-dwelling form of *Hastigerina pelagica*, as *H. pelagica* has a distinct habitat depth and biogeographic range. Ecologically, *H. pelagica* is a tropical, surface-dwelling species and occurs in shallow waters of ∼ 16–29°C (Bé and Tolderlund

1971; Hemleben et al. 1989). In contrast, *Hastigerina* sp. is found in ∼ 7°C waters at mesopelagic depths. Furthermore, while we captured 14 *Hastigerina* sp. on four ROV sampling trips, no surface water *H. pelagica* are reported off Southern California by 28 depth-stratified plankton net tows across seasons from 2000 to 2002 (Field 2004), by 28 yr of blue-water diving for planktonic foraminifera in the Davidson Current (June–September; H. J. Spero pers. comm.), by a biogeographic survey of the planktonic
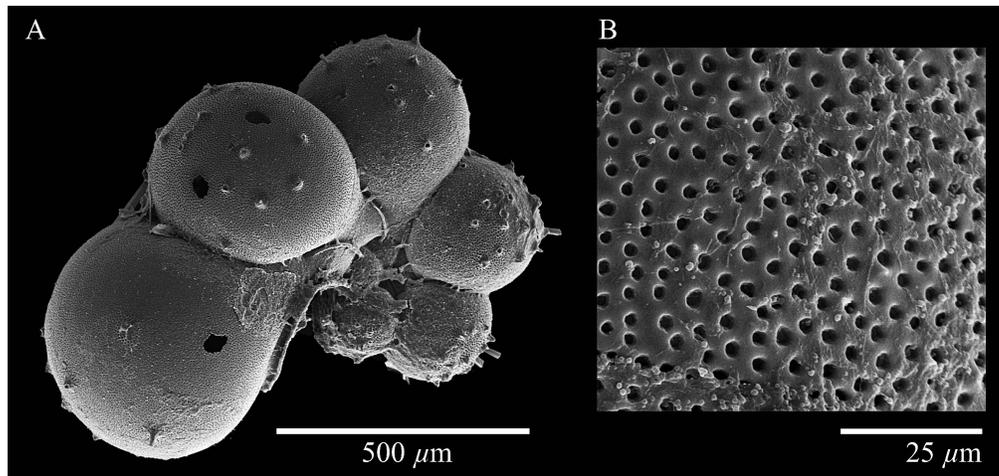
Fig. 4.   Scanning electron microscope (SEM) images of *Hastigerina* sp. (A) *Hastigerina* sp. with only spine bases visible; note the relatively sparse and even distribution of spines, as compared to *H. digitata* (Fig. 3). (B) Typical wall structure.

foraminifera of the North Pacific (Bradshaw 1959), or by sediment traps off Southern California (Sautter and Thunell 1991).

Morphologically, *Hastigerina* sp. has a slower rate of chamber enlargement, an umbilicus that shows the apertural lips of early chambers, and more pie-shaped chambers than the holotype of *H. pelagica*. However, it can be argued that the mesopelagic *Hastigerina* sp. falls at the far end of the morphological range of specimens attributed to *H. pelagica* in past studies. Genetic studies are thus needed to resolve the relationship between *Hastigerina* sp. and *H. pelagica*. The unique ecology and biogeographic range of *Hastigerina* sp. and the presence of cryptic genetic species in all planktonic foraminiferal species studied to date (Darling and Wade 2008) strongly argue against the inclusion of Monterey Bay *Hastigerina* sp. within *H. pelagica* at the present time.

Depth distribution—During the period of our study, video signatures of *H. digitata* had a characteristic depth distribution over the Monterey Canyon, with a median depth of 312 m and an interquartile range (IQR) of 78 m (Fig. 2, transit$_{non-standardized}$ observations = 9614, mean depth = 375 m, standard deviation = 344 m). We found the depth distribution of large, adult *H. digitata* to be narrower than would be expected of a normal distribution (Lilliefors test for normality, $p < 0.001$ for transit$_{non-standardized}$ and transect$_{quantitative}$ data). The core depth range, bounded by the 25th and 75th quartiles, of *H. digitata* was 280–358 m (Fig. 2A). This core range was located above the oxygen minimum zone in Monterey Bay, which has oxygen concentrations below 0.5 mL L^{-1} at depths between ~ 500 and 800 m. The interquartile of the *H. digitata* population corresponded with a range in mean annual temperature of 0.6°C (7.8–7.2°C), a salinity of 0.03 (34.18–34.21), a potential density of 0.11 (26.65–26.77), and oxygen of 0.33 (1.35–1.02 mL L^{-1}) (Fig. 2B).

We recorded a number of extremely deep observations (Fig. 2), with 3% of *H. digitata* found below 865 m, and the deepest at 3512 m. Each of these deep observations was

confirmed as a typical *H. digitata* video observation by the authors. We have yet to collect deep specimens to determine if they are the same species and if they are living individuals.

Given the small size of the second midwater species, *Hastigerina* sp., our depth-linked observations are limited to those confirmed with a slowed or stopped ROV in September 2008, November and December 2009, and March 2010, at depths between 200 and 400 m. We think it unlikely that *Hastigerina* sp. has a primarily shallow depth distribution, given the lack of mature *Hastigerina* in shallower waters (0–200 m) in previous studies (Bradshaw 1959; Field 2004). Similarly, we also think it unlikely that *Hastigerina* sp. is highly abundant below 400 m. ROV transit$_{non-standardized}$ observations are often recorded from a slowed or stopped ROV (conditions in which *Hastigerina* sp. can be observed), and we report a general lack of transit$_{non-standardized}$ observations below this depth.

Seasonality in depth—A pairwise Wilcoxon rank sum test indicated two main depth distribution modes for *H. digitata* over the Monterey Canyon (Fig. 5A). In the months from March to June, the median depth of *H. digitata* occurred at 301 m. From September through January, *H. digitata* had a relatively deep median depth of 329 m. Transitional months (July, August, and February) include months that conflicted pairwise with monthly depth distributions from either the shallow or deep modes (Table 1). The shallow and deep seasons could also be subdivided in a slightly different manner based on the Wilcoxon rank sum results, with the shallow season extending from February to May and with June joining the transitional months of July and August (Fig. 5A).

Median monthly depth was significantly correlated to four environmental parameters: temperature, salinity, density, and upwelling (Table 2, Spearman's rank correction, $p < 0.05$). Median monthly depth was best correlated with temperature, salinity, and density at 60 m, a depth chosen to be maximally sensitive to changes in thermocline depth. The single best correlate of *H. digitata* median
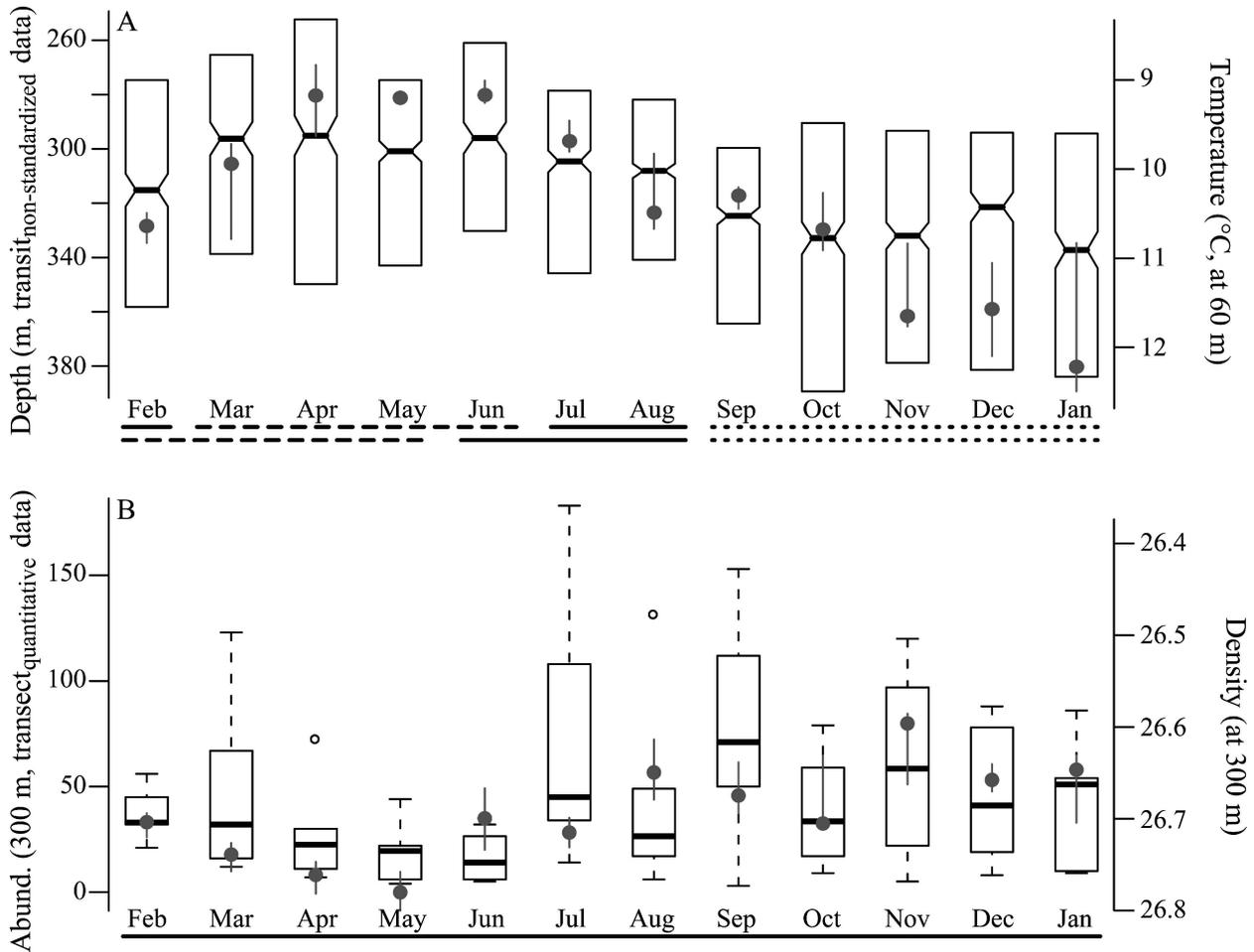
Fig. 5. (A) Seasonal depth distribution (transit $_{\text{non-standardized}}$ data) and (B) abundance (abund.) of *H. digitata* (transect$_{\text{quantitative}}$ data at 300 m) shown as box plots. (A) Heavy black horizontal bars indicate median, notches extended to $\pm$ 1.58 $\times$ IQR/$\sqrt{n}$, tops and bottoms of boxes delineate the IQR, (B) dashed whiskers extended up to 1.5 $\times$ IQR beyond the box, and outliers are shown as open dots (whiskers and outliers not shown in A to allow the main trend in median and IQR to be seen). The medians of the best environmental correlates of (A) depth distribution (temperature at 60 m) and (B) population abundance (density at 300 m) are shown as solid dots, with solid bars extending to the upper and lower quartiles, respectively. The two rows of black bars beneath the y-axis in (A) indicate two grouping options for *H. digitata* depth distributions based on results in Table 1: long dashes indicate shallow distributions, the short dashes indicate deep distributions, and the solid line indicates transitional months between the shallow and deep modes. No significant differences among months were found in B, as indicated by the solid line below the y-axis.

population depth was temperature at 60 m (Fig. 5A, ρ = 0.90 and p = 0.000).

Seasonality in population abundance—In contrast to the seasonality detected in the depth distribution of *H. digitata*, we did not find comparable statistical support for seasonality in the population abundance at 300 m in depth for the same time period (Fig. 5B). For all pairwise Wilcoxon comparisons with a Bonferroni correction for multiple comparisons, we did not reject the null hypothesis of no difference between months. However, here the Wilcoxon test had low power to detect differences among months as a result of the limited number of repeated monthly observations (four to seven repeated observations of any given month between 2002 and 2008). Our results were unchanged by including all observations between 1997 and 2008 and were not driven by the strict nature of the Bonferroni correction.

The general increase in median population abundance between June and January (Fig. 5B) was significantly correlated with two environmental parameters using Spearman's rank correlation (Table 2). Between the two parameters, temperature and density at 300 m, the best correlate was density (Fig. 5B, ρ = -0.692 and p = 0.016).

Determinants of population abundance—We examined two types of correlates of *H. digitata* abundance over the 12-yr time series: (1) past standing abundance and population dynamics of *H. digitata* and (2) environmental conditions and dynamics. The change in *H. digitata* abundance at 300 m from one month to the next (abundance$_{\text{month}}$ − abundance$_{\text{month−1}}$) was the best predictor of subsequent population dynamics. The change in abundance from a given month to the next was negatively correlated with the change in abundance in the following month (Pearson's r = -0.44

Table 1. Wilcoxon pairwise rank sum test of the depth distribution of *Hastigerinella digitata* by month with a Bonferroni correction for multiple comparisons. *p*-values with values of less than 0.05 are indicative of a significant difference in depth distribution between months. Italic indicates significance at the $p < 0.01$ level, and bold font indicates significance at the $p < 0.05$ level.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Feb	*0.000*	—	—	—	—	—	—	—	—	—	—
Mar	*0.000*	0.544	—	—	—	—	—	—	—	—	—
Apr	*0.000*	0.232	1.000	—	—	—	—	—	—	—	—
May	*0.000*	1.000	1.000	1.000	—	—	—	—	—	—	—
Jun	*0.000*	**0.014**	1.000	1.000	0.153	—	—	—	—	—	—
Jul	*0.000*	1.000	0.376	**0.040**	1.000	*0.006*	—	—	—	—	—
Aug	*0.000*	1.000	*0.009*	*0.000*	0.240	*0.000*	1.000	—	—	—	—
Sep	1.000	*0.001*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	—	—	—
Oct	1.000	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	1.000	—	—
Nov	1.000	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	1.000	1.000	—
Dec	1.000	*0.009*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	1.000	1.000	1.000

and $p < 0.001$) and was well correlated to the change in abundance from one month to the next, 6 months hence (Pearson's $r = 0.379$ and $p = 0.003$). Additionally, the temporal autocorrelation in standing abundance was significant at a $p < 0.05$ significance level for up to 2 months (1 month: $r = 0.32$; 2 month: $r = 0.25$), with a stronger correlation with standing abundance 6 months prior (Pearson's $r = 0.42$ and $p < 0.001$).

A number of environmental variables were significantly correlated with the abundance of *H. digitata*, although the correlation coefficient was generally less than 0.30, with one exception. A change in spiciness at 300 m was correlated to a change in *H. digitata* abundance in the following month, with $r = -0.30$ ($p = 0.017$). Temperature and spiciness (surface and 300 m) were significant negative correlates of *H. digitata* abundance at 4–5-month lags, with correlations between -0.22 and -0.283 (*see* also Fig. 6),

supporting the negative correlation between temperature and density and abundance on a seasonal cycle. There was also supporting evidence of an approximately half-year lagged correlation between environmental parameters and population abundance. The abundance of *H. digitata* was correlated to the NPGO, NOI, and surface-water spiciness 6 months prior ($r = 0.29$, 0.20, and -0.25, with $p = 0.002$, 0.036, and 0.026, respectively).

Across all 12 yr, *H. digitata* had a median abundance of 27 observations (obs.) per 1400 m^3 transected ($\sim$ 1 obs. every 51 m^3), an interquartile range of 11–55 observations per 1400 m^3 ($\sim$ 1 obs. every 25–127 m^3), and a maximum abundance of 314 observations per 1400 m^3 ($\sim$ 1 obs. per 4.5 m^3).

Observations of live specimens and interspecific interactions—When live specimens were collected by the ROV,

Table 2. Correlation of the median monthly depth and population abundance of *Hastigerinella digitata* with eight environmental parameters. Five parameters (temperature, salinity, density, oxygen, and spiciness) are measured at multiple depths: surface (10 m), thermocline (60 m), and population depth (300 m). Correlations were tested using Spearman's rank correlation (ρ); italic indicates significance at the $p < 0.01$ level, and bold font indicates significance at the $p < 0.05$ level.

| Variable	Depth (m)	Depth distribution Spearman (ρ)	Depth distribution Spearman (p)	Population abundance Spearman (ρ)	Population abundance Spearman (p)
Temperature	10	*0.846*	*0.001*	0.503	0.099
	60	*0.902*	*0.000*	0.455	0.140
	300	**0.664**	**0.022**	**0.657**	**0.024**
Salinity	10	-0.524	0.084	-0.119	0.716
	60	*-0.867*	*0.000*	-0.434	0.161
	300	-0.545	0.071	-0.566	0.059
Density	10	*-0.867*	*0.000*	-0.420	0.177
	60	*-0.888*	*0.000*	-0.469	0.127
	300	*-0.664*	*0.022*	**-0.692**	**0.016**
Stratification	—	-0.427	0.169	0.000	1.000
Oxygen	10	0.294	0.354	-0.007	0.991
	60	0.510	0.094	0.168	0.604
	300	0.497	0.104	0.140	0.667
Transmissometry	—	-0.133	0.680	-0.042	0.897
Spiciness	10	0.552	0.067	0.510	0.094
	300	0.224	0.485	0.364	0.246
Upwelling	—	*-0.762*	*0.006*	-0.343	0.276
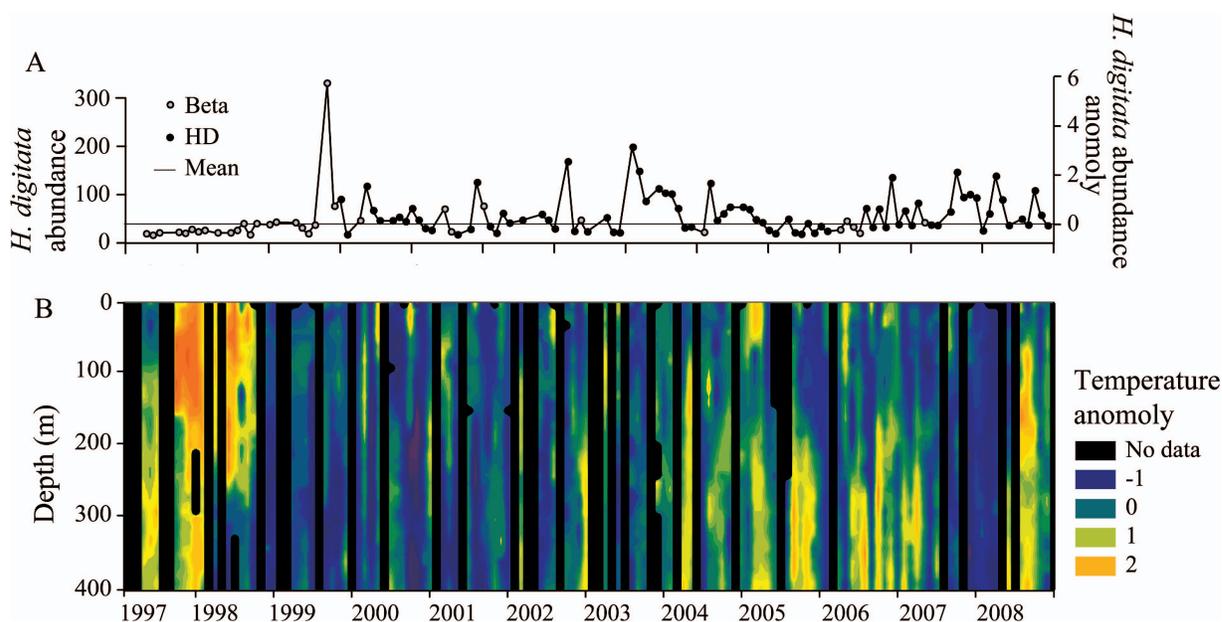
Fig. 6. Long-term record of *H. digitata* abundance at 300-m depth and corresponding temperature anomalies spanning the same time period over the Monterey Canyon. (A) Total observed *H. digitata* from effort-standardized transects at 300 m depth in BetaCam (open circles) and HD (solid circles) tapes (right axis shows abundance anomaly scale). (B) Temperature anomalies by depth for the same time interval from 0 to 400 m.

extensions of their cytoplasm, rhizopodia, reached to twice the length of the spines and were sometimes tangled with each other (Fig. 1F). These cytoplasmic 'fishing lines' were apparent on video and in the laboratory by their waving motion, which contrasted with that of the relatively stiff spines (Fig. 1F,G). We were not able to determine whether one or three rhizopods extend from each spine tip, as may be possible given the triradiate spine structure. With handling, or sometimes during collection with strong suction, the rhizopoda were withdrawn and the bubble network was disturbed (Fig. 1C,D). Individual bubbles of the cytoplasmic bubble network of *H. digitata* were roughly teardrop-shaped, with the narrow ends appearing to extend out from the tips of the digitate projections (Fig. 1A). Spines projected both through and between individual bubbles, and the sides of the bubbles deformed to form angles where they were pressed against adjacent bubbles. This differed from bubbles found around *Hastigerina* sp., which were spherical, were not deformed where they contacted other bubbles, and did not each appear to extend directly from the test (Fig. 1B). The cytoplasmic bubble network extended from 0.4 to 1.2 mm beyond the edge of *H. digitata* and *Hastigerina* sp. tests. Specimens were maintained for 2 weeks in the lab in still, filtered collection water at 6°C and appeared healthy for between 2 d and the full duration of the study.

We observed several interspecific interactions among captured and in situ specimens of *H. digitata*. At least 41% of *H. digitata* were found in association with copepods, and occasionally ostracods, when collected (Fig. 1G). The copepods appeared to be in various stages of digestion, from recently captured, still-moving individuals to empty, translucent carapaces. Small crustaceans that were not new captures were contacted by numerous rhizopodia

(Fig. 1G), and many were drawn well in between the spines and held up tight to the margin of the bubble network or between the outer margins of the bubbles. Crustaceans held by *H. digitata* that were maintained in the lab were cleared within 3 d, and the empty carapaces dropped off the foraminifer. We attempted to feed by-catch copepods to *H. digitata* in the lab but were not able to observe a capture. However, copepods left in a container with *H. digitata* overnight had been captured by morning.

A few interspecific associations have been captured on video, including the encounter of a holopelagic isopod (*Acanthamunnopsis milleri*) with *H. digitata*. In this encounter *A. milleri* and *H. digitata* were in contact when first discovered and were still for a few seconds; this was followed by *A. milleri* initiating an escape response (swimming vigorously and pushing, sweeping its free legs down along the legs that were in contact with the foraminifera), with the *H. digitata* in tow. An agalmid siphonophore and the narcomedusa, *Aegina citrea* has also been observed attached to *H. digitata*, although in these cases it is unlikely that *H. digitata* was the predator, based on past diet studies of planktonic foraminifera (Anderson et al. 1979; Caron and Be 1984).

Discussion

Mesopelagic foraminifera over Monterey Canyon—Both midwater species found over Monterey Canyon—*H. digitata* and *Hastigerina* sp.—are clearly allied with a species that dwells near the surface, *H. pelagica*, which has been studied in some detail using SCUBA and has been observed in cultures and sediments (Anderson and Be 1976; Spindler et al. 1979; Loncaric et al. 2005). All three species have (1) lightly calcified, monolamellar tests, (2) distinctive,

heavily calcified triradiate spines (Figs. 3, 4; seen in no other living foraminifera), and (3) a bubble network encapsulating the test (Fig. 1A,B). While the presence of a cytoplasmic bubble capsule is well known from *H. pelagica*, this is the first report of a comparable cytoplasmic bubble capsule in *H. digitata*. This is also the first report of a deep-water species, *Hastigerina* sp., that is morphologically similar to *H. pelagica*.

H. digitata and *Hastigerina* sp. of Monterey Bay differ from the *H. pelagica* holotype in possessing (1) six to eight (rather than five to six) chambers in the last open whorl, (2) a more open coiled, evolute shell, (3) larger maximum test sizes, (4) a mesopelagic rather than epipelagic depth distribution (Figs. 3, 4), and (5) a different temperature range. *H. pelagica* is reported from the California Current from only a few locations off Baja California (Bradshaw 1959) and is generally circumglobal in tropical and subtropical surface waters (~ 16–29°C; Bé and Tolderlund 1971; Hemleben et al. 1989). Here, we observed *H. digitata* and *Hastigerina* sp. in far cooler water ($\sim 7^{\circ}$C). In collected individuals, we observed test diameters (not including the spines) of up to 3.4 mm in *H. digitata* and of ~ 1.7 mm in *Hastigerina* sp., in contrast to maximum test diameters of ~ 1 mm in *H. pelagica* (Anderson and Be 1976). *H. digitata* is the largest modern planktonic foraminifer; we calculate spherical volumes of roughly 3.5 cm^3, including spines, or 287 cm^3, if considering the volume they occupy with extended rhizopodia.

Trophic ecology of H. digitata—Our in situ and laboratory observations provide support for the suggestion that *H. digitata* is exclusively carnivorous (Rhumbler 1911; C. Hemleben pers. comm. [as cited in Coxall et al. 2007]). We observed at least 15 specimens with ensnared copepods in various stages of digestion, and more than half of these were attached to more than one copepod. These observations are similar to those reported for *H. pelagica*, which has been argued to be exclusively carnivorous based on similar feeding experiments and field observations (Anderson et al. 1979; Spindler et al. 1984; Anderson 1996).

Large aggregates of marine snow are abundant at a depth of 300 m over the Monterey Canyon. Detritivorous plankton like phaeodarians (holopelagic Cercozoans, previously grouped with radiolarians) are consistently observed covered in a blanket of marine snow (S. H. D. Haddock pers. comm.). In contrast, *H. digitata* and *Hastigerina* sp. do not accumulate particulate matter on their spines, aside from up to four copepod carapaces, despite the abundance of surrounding marine snow in the water column. Thus, it appears unlikely that marine snow comprises a meaningful portion of the diet of either *Hastigerina* sp. or *H. digitata*.

Habitat depth of H. digitata—Our transit data show that the bulk of the *H. digitata* population was located within a ~ 78-m interval around a median depth of 312 m, corresponding to a range in mean annual temperature from 7.2°C to 7.8°C and an oxygen concentration from 1 to 1.3 mL L^{-1} (Fig. 2). *H. digitata* is one of a few modern representatives of more than 130 million yr of digitate

foraminifera, many of which are hypothesized to live or have lived in association with oxygen minimum zones. This association is based on inferences from δ^{13}C and δ^{18}O from both living and fossil digitate planktonic foraminifera, oblique plankton tows, and a correspondence between abundant, diverse digitate fauna and locations or periods characterized by stable, expanded oxygen minimum zones (Coxall et al. 2007). Existing evidence generally places the habitat depth of digitate planktonic foraminifera deeper than that of other conspecific planktonic foraminifera, but it does not provide specific evidence constraining the habitat depth of digitate foraminifera relative to the oxygen minimum zone proper. In this context, our findings place a modern constraint on the habitat depth of *H. digitata* (above the core of the oxygen minimum zone) that can be used to calibrate and interpret geochemical records of other species.

H. digitata's depth range appears to be the narrowest described to date for mesopelagic fauna within Monterey Bay. *H. digitata* has a slightly narrower depth range than the mesopelagic scyphomedusae *Atolla*, *Periphylla*, and *Poralia* (Osborn et al. 2007), which have narrower depth distributions than the physonect siphonophore *Nanomia bijuga* (Robison et al. 1998) and calycophoran siphonophores (principally *Chuniphyes multidentata* and *Lensia conoidea*; Silguero and Robison 2000). However, the broader depth ranges in the calycophoran siphonophores may be driven in part by averaging across seasonal changes in habitat depth, rather than by a broader habitat range at a given time, by lumping species together, and/or by active swimming. We report a seasonal change in *H. digitata* depth as well, with shallower occurrences coinciding with upwelling (Fig. 5A, corresponding with cooler temperatures at 60 m), but the shift in median depth from 301 to 329 m is modest compared to those observed in calycophoran siphonophores (Silguero and Robison 2000, from 300–400 m to 700–800 m). By moving into shallower waters as upwelling intensifies, *H. digitata* populations appear to track and experience a relatively consistent oceanographic environment throughout the year.

We propose two hypotheses to account for the constrained depth distribution and modest seasonal depth fluctuations in *H. digitata*. First, *H. digitata* may be positioned to maximize encounters and capture of copepods and other prey. The habitat depth of *H. digitata* approximately coincides with a peak in mesopelagic biomass (Saltzman and Wishner 1997*a,b*; Criales-Hernandez et al. 2008) and, specifically, in mesopelagic calanoid copepods (Mauchline 1998). In feeding experiments and observations, omnivorous and carnivorous planktonic foraminifera have been shown to prey predominantly on copepods, in keeping with the copepods' relatively high abundance (Anderson et al. 1979; Caron and Be 1984; Swanberg and Caron 1991), and to prefer calanoid copepods over other copepod taxa (Spindler et al. 1984). While calanoid abundances decrease with water depth, they are generally abundant in the upper 300 m and decrease irregularly to 1000 m (Mauchline 1998). In Monterey Bay, a ~ 300-m habitat depth likely coincides with a peak in mesopelagic biomass above the oxygen minimum zone

(Saltzman and Wishner 1997*a,b*; Criales-Hernandez et al. 2008), a peak in mesopelagic copepod abundance (Childress 1977; Thuesen et al. 1998), the diel ambits of vertically migrating copepods (Huntley and Brooks 1982; Hattori 1989), deep ontogenetic or seasonal phases of the dominant epipelagic copepods like *Calanus pacificus* or *Metridia pacifica* (Batchelder 1985; Ohman et al. 1998; Johnson and Checkley 2004), and the margin between the lower edge of the California Current and the upper extent of the California Undercurrent.

In general, by having a population centered above the oxygen minimum zone, *H. digitata,* like many gelatinous mesopelagic predators studied to date (*Nanomia bijuga* [Robison et al. 1998], calycophoran siphonophores [Silguero and Robison 2000], and *Atolla*, the most abundant of the scyphomedusae [Osborn et al. 2007]), has an abundant and diverse potential prey field. This may account for *H. digitata*'s relatively small seasonality in habitat depth and abundance. Finally, while the center of the vertical distribution of *H. digitata* may be determined based on relative food availability, the range may be affected by interspecific interactions such as competition and predation.

The stable depth distribution of *H. digitata* through years and conditions under which other taxa showed distinctly altered depth distributions and abundances indicates that prey availability alone may not explain the depth range of large *H. digitata*. Thus, our second hypothesis is that *H. digitata* is tightly clustered in space in order to maintain high-enough population densities for sexual reproduction. Planktonic foraminifera, unlike their benthic relatives, are thought to reproduce only via sexual reproduction and must undergo gametogenesis in close enough proximity to other individuals in the same species for gametes from two different parents to fuse (Hemleben et al. 1989; Bijma et al. 1990). *H. digitata*'s close relative, *H. pelagica*, achieves this feat by reproducing on a lunar cycle (Spindler et al. 1978, 1979; Loncaric et al. 2005), between 15:00 h and 18:00 h (Spindler et al. 1978, 1979), at $\sim$ 200 m in depth (Hemleben and Spindler 1983; Hemleben et al. 1989). Loncari et al. (2005) hypothesized that the combined life-history characteristics of carnivory and lunar reproduction explain the relative consistent population abundance of *H. pelagica,* as compared to the highly seasonal abundances of other spinose planktonic foraminifera. We can now add that the carnivorous *H. digitata* also has relatively constant abundance throughout the year, with the highest numbers, on average, occurring between July and November, but we are unable to comment on the periodicity of reproduction.

The mechanisms by which planktonic foraminifera synchronize gametogenesis are not well understood (Hemleben et al. 1989). *H. pelagica* that were taken into culture more than 13 d before the full moon typically failed to undergo gametogenesis, a pattern Spindler et al. (1979) hypothesized was caused by a failure in the needed trigger of "external coincidences superimposed on the internal clock." However, if the narrow depth range of *H. digitata* is indeed for reproductive purposes, we speculate that this may be maintained by a possible population-level control of depth distribution and the timing and onset of reproduction via quorum sensing (or self-organizing behavior). Quorum sensing is known from bacteria, yeast, and social insects, among others (Miller and Bassler 2001; Sprague and Winans 2006; Visscher 2007), and has been hypothesized in the regulation of marine diatom populations (Falciatore and Bowler 2002).

Population dynamics of H. digitata—*H. digitata* was continuously present at approximately 300 m in depth above Monterey Canyon for all 115 months surveyed between 1997 and 2008 (Fig. 6). Weak seasonality and environmental correlations both point to a negative correlation between temperature and other upwelling indicators and the abundance of *H. digitata*. Seasonally increased stratification (Fig. 5B) and years with unusual cool water temperatures (Fig. 6) both weakly predicted increases in *H. digitata*. In addition, the standing population of *H. digitata* and the prevailing environmental conditions were good predictors of *H. digitata* abundance 6 months later, also supporting a weak seasonality in abundance.

Previous studies of mesopelagic biota in the Monterey Canyon have found stronger evidence of seasonality in population abundance and/or habitat depth (Robison et al. 1998; Silguero and Robison 2000). It is possible that the lack of strong seasonality and detection of long-term determinants in *H. digitata* populations at 300 m were related to sampling, including the depth interval sampled, and detection of only the largest *H. digitata* in video transects. We rule out the possibility of video detection bias on two grounds. We found a high repeatability in transect counts of *H. digitata* between different annotators. Additionally, we rejected the null hypothesis of random variations in *H. digitata* abundance using a runs test, which we interpret as further evidence against the theory that video detection problems alone drove the observed population variation in *H. digitata*. However, slight shifts in *H. digitata*'s narrow depth range may have impeded our ability to track all variations in population abundance. For instance, we found, on average, an increase in the median abundance and the interannual variability of *H. digitata* abundance at 300 m during the non-upwelling season. During this season *H. digitata* populations resided at a median depth of 321 m, deeper than the 301-m median depth in the upwelling season. In effect, the weak seasonal increase in abundance we described is likely to be dampened relative to the actual or increased population size during that season.

H. digitata thus provides insight into another successful mesopelagic life-history strategy. They are planktivorous sit-and-wait predators that live in a relatively dense curtain from 280 to 358 m in depth, and they prey primarily upon copepods throughout the year. We observed a median abundance of $\sim$ 1 *H. digitata* 51 m^{-3} in the 300-m depth transects$_{quantitative}$. If we make the conservative estimate that the largest individuals comprise 10% of the population (likely a large overestimate, given the typical size structure of living populations; Berger 1971), then on average there is $\sim$ 1 mesopelagic foraminifera every 5 m^3 in Monterey Bay

at 300 m in depth, and occasionally there are more than 2 individuals m^{-3}. Fluctuations in population abundance appear to be weakly linked to environmental conditions, but they do not show the same level of seasonality measured for other mesopelagic predators. While this is surprising in light of the highly seasonal environment, it corresponds with the similar population dynamics and trophic ecology of the closely related species *H. pelagica* (Anderson et al. 1979; Spindler et al. 1984; Loncaric et al. 2005). *H. pelagica* is also carnivorous and lacking strong evidence of seasonal population dynamics. With their continuous presence in the mesopelagic realm and peak in population abundance in fall rather than summer, *H. digitata* may provide an important source of mortality for small copepods when other mesopelagic planktivorous predators are rare. Finally, these observations provide the first detailed examination of the depth distribution and population dynamics of adult mesopelagic foraminifera and provide a basis for understanding morphologically similar species and their environmental context in the fossil record.

References

ANDERSON, O. R. 1996. The physiological ecology of planktonic sarcodines with applications to paleoecology: Patterns in space and time. J. Eukaryot. Microbiol. **43:** 261–274, doi:10.1111/j.1550-7408.1996.tb03989.x

———, AND A. W. H. BÉ. 1976. A cytochemical fine structure study of phagotrophy in a planktonic foraminifer, *Hastigerina pelagica* (d'Orbigny). Biol. Bull. **151:** 437–449, doi:10.2307/1540498

———, M. SPINDLER, A. W. H. BÉ, AND C. HEMLEBEN. 1979. Trophic activity of planktonic foraminifera. J. Mar. Biol. Assoc. UK **59:** 791–799, doi:10.1017/S002531540004577X

BANNER, F. T., AND W. H. BLOW. 1959. The classification and stratigraphical distribution of the Globigerinaceae. Palaeontology **2:** 1–27.

BATCHELDER, H. P. 1985. Seasonal abundance, vertical distribution, and life history of *Metridia pacifica* (Copepoda: Calanoida) in the oceanic subarctic Pacific. Deep-Sea Res. **32:** 949–964.

BÉ, A. W. H. 1977. An ecological, zoogeographic and taxonomic review of recent planktonic foraminifera, p. 1–100. *In* A. T. S. Ramsay [ed.], Oceanic micropalaeontology. Academic Press.

———, C. HEMLEBEN, O. R. ANDERSON, M. SPINDLER, J. HACUNDA, AND S. TUNTIVATE-CHOY. 1977. Laboratory and field observations of living planktonic foraminifera. Micropaleontology **23:** 155–179, doi:10.2307/1485330

———, AND D. S. TOLDERLUND. 1971. Distribution and ecology of living planktonic foraminifera in surface waters of the Atlantic and Indian Oceans, p. 105–149. *In* B. M. Funnell and W. K. Riedel [eds.], Micropaleontology of marine bottom sediments. Cambridge Univ. Press.

BERGER, W. H. 1971. Sedimentation of planktonic foraminifera. Mar. Geol. **11:** 325–358, doi:10.1016/0025-3227(71)90035-1

BIJMA, J., J. EREZ, AND C. HEMLEBEN. 1990. Lunar and semi-lunar reproductive cycles in some spinose planktonic foraminifers. J. Foraminifer. Res. **20:** 117–127, doi:10.2113/gsjfr.20.2.117

BISHOP, J. K. B. 1999. Transmissometer measurement of POC. Deep-Sea Res. I **46:** 353–369, doi:10.1016/S0967-0637(98)00069-7

BRADSHAW, J. S. 1959. Ecology of living planktonic foraminifera in the North and Equatorial Pacific Ocean. Contrib. Cushman. Found. Foramanifer. Res. **10:** 25–64.

BRADY, H. B. 1879. Notes on some of the reticularian Rhizopoda of the Challanger Expedition II: Additions to the knowledge of porcellaneous and hyaline types. Q. J. Microsc. Sci. **19:** 261–299.

CARON, D. A., AND A. W. H. BÉ. 1984. Predicted and observed feeding rates of the spinose planktonic foraminifer *Globigerinoides sacculifer*. Br. Mar. Sci. **35:** 1–10.

CHELTON, D. B. 1984. Seasonal variability of alongshore geostrophic velocity off central California. J. Geophys. Res. Oceans **89:** 3473–3486, doi:10.1029/JC089iC03p03473

CHILDRESS, J. J. 1977. Effects of pressure, temperature and oxygen on oxygen-consumption rate of midwater copepod *Gaussia princeps*. Mar. Biol. **39:** 19–24, doi:10.1007/BF00395588

CIFELLI, R. 1969. Radiation of Cenozoic planktonic foraminifera. Syst. Zool. **18:** 154–168, doi:10.2307/2412601

COLLINS, C. A., J. T. PENNINGTON, C. G. CASTRO, T. A. RAGO, AND F. P. CHAVEZ. 2003. The California Current System off Monterey, California: Physical and biological coupling. Deep-Sea Res. II **50:** 2389–2404, doi:10.1016/S0967-0645(03)00134-6

COXALL, H. K., P. A. WILSON, P. N. PEARSON, AND P. E. SEXTON. 2007. Iterative evolution of digitate planktonic foraminifera. Paleobiology **33:** 495–516, doi:10.1666/06034.1

CRIALES-HERNANDEZ, M. I., R. SCHWAMBORN, M. GRACO, P. AYON, H. J. HIRCHE, AND M. WOLFF. 2008. Zooplankton vertical distribution and migration off Central Peru in relation to the oxygen minimum layer. Helgoland Mar. Res. **62:** S85–S100, doi:10.1007/s10152-007-0094-3

DARLING, K. F., AND C. M. WADE. 2008. The genetic diversity of planktic foraminifera and the global distribution of ribosomal RNA genotypes. Mar. Micropaleontol. **67:** 216–238, doi:10.1016/j.marmicro.2008.01.009

———, ———, D. KROON, AND A. J. L. BROWN. 1997. Planktic foraminiferal molecular evolution and their polyphyletic origins from benthic taxa. Mar. Micropaleontol. **30:** 251–266, doi:10.1016/S0377-8398(96)00057-6

DE VARGAS, C., L. ZANINETTI, H. HILBRECHT, AND J. PAWLOWSKI. 1997. Phylogeny and rates of molecular evolution of planktonic foraminifera: SSU rDNA sequences compared to the fossil record. J. Mol. Evol. **45:** 285–294, doi:10.1007/PL00006232

DI LORENZO, E., AND OTHERS. 2008. North Pacific Gyre Oscillation links ocean climate and ecosystem change. Geophys. Res. Lett. **35:** 1–6, L08607, doi:10.1029/2007GL032838

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, doi:10.1038/298841a0

FALCIATORE, A., AND C. BOWLER. 2002. Revealing the molecular secrets of marine diatoms. Annu. Rev. Plant Biol. **53:** 109–130, doi:10.1146/annurev.arplant.53.091701.153921

FIELD, D. B. 2004. Variability in vertical distributions of planktonic foraminifera in the California Current: Relationships to vertical ocean structure. Paleoceanography **19:** 1–22, PA2014, doi:10.1029/2003PA000970

FLAMENT, P. 2002. A state variable for characterizing water masses and their diffusive stability: Spiciness. Prog. Oceanogr. **54:** 493–501, doi:10.1016/S0079-6611(02)00065-4

HADDOCK, S. H. D. 2007. Comparative feeding behavior of planktonic ctenophores. Integr. Comp. Biol. **47:** 847–853, doi:10.1093/icb/icm088

HATTORI, H. 1989. Biomodal vertical distribution and diel migration of the copepods *Metridia pacifica*, *M. okhotensis* and *Pleuromamma scutullata* in the western North Pacific Ocean. Mar. Biol. **103:** 39–50, doi:10.1007/BF00391063

HEMLEBEN, C., AND M. SPINDLER. 1983. Lebenszyklus der planktonischen Foraminifera *Hastigerina pelagica* (d'Orbigny). Institute for Scientific Films. [Life cycle of the planktonic foramininifera *Hastigerina pelagic* (d'Orbigny).]

———, ———, AND O. R. ANDERSON. 1989. Modern planktonic foraminifera. Springer-Verlag.

HSIEH, C. H., C. ANDERSON, AND G. SUGIHARA. 2008. Extending nonlinear analysis to short ecological time series. Am. Nat. **171:** 71–80, doi:10.1086/524202

———, S. M. GLASER, A. J. LUCAS, AND G. SUGIHARA. 2005a. Distinguishing random environmental fluctuations from ecological catastrophes for the North Pacific Ocean. Nature **435:** 336–340, doi:10.1038/nature03553

———, AND M. D. OHMAN. 2006. Biological responses to environmental forcing: The linear tracking window hypothesis. Ecology **87:** 1932–1938, doi:10.1890/0012-9658(2006)87[1932:BRTEFT]2.0.CO;2

———, AND OTHERS. 2005b. A comparison of long-term trends and variability in populations of larvae of exploited and unexploited fishes in the Southern California region: A community approach. Prog. Oceanogr. **67:** 160–185, doi:10.1016/j.pocean.2005.05.002

HUNTLEY, M., AND E. R. BROOKS. 1982. Effects of age and food availability on diel vertical migration of *Calanus pacificus*. Mar. Biol. **71:** 23–31, doi:10.1007/BF00396989

JOHNSON, C. L., AND D. M. CHECKLEY. 2004. Vertical distribution of diapausing *Calanus pacificus* (Copepoda) and implications for transport in the California undercurrent. Prog. Oceanogr. **62:** 1–13, doi:10.1016/j.pocean.2004.08.001

LIPPS, J. H. 1979. Ecology and paleoecology of planktic foraminifera, p. 62–104. *In* J. H. Lipps, W. H. Berger, M. A. Buzas, R. G. Douglas, and C. A. Ross [eds.], Foraminiferal ecology and paleoecology, SEPM Short Course Notes 6. Society of Economic Paleontologists & Mineralogists.

LONCARIC, N., G. J. A. BRUMMER, AND D. KROON. 2005. Lunar cycles and seasonal variations in deposition fluxes of planktic foraminiferal shell carbonate to the deep South Atlantic (central Walvis Ridge). Deep-Sea Res. I **52:** 1178–1188, doi:10.1016/j.dsr.2005.02.003

LONGET, D., AND J. PAWLOWSKI. 2007. Higher-level phylogeny of Foraminifera inferred from the RNA polymerase II (RPBI) gene. Eur. J. Protistol. **43:** 171–177, doi:10.1016/j.ejop.2007.01.003

LYNN, R. J., AND J. J. SIMPSON. 1987. The California Current System: The seasonal variability of its physical characteristics. J. Geophys. Res. Oceans **92:** 12947–12966, doi:10.1029/JC092iC12p12947

MAUCHLINE, J. 1998. The biology of calanoid copepods. Academic Press.

MILLER, M. B., AND B. L. BASSLER. 2001. Quorum sensing in bacteria. Annu. Rev. Microbiol. **55:** 165–199, doi:10.1146/annurev.micro.55.1.165

NATIONAL RESEARCH COUNCIL (NRC). 2003. Future needs in deep submergence science: Occupied and unoccupied vehicles in basic ocean research. National Academy Press.

NORRIS, R. D. 1991. Biased extinction and evolutionary trends. Paleobiology **17:** 388–399.

OHMAN, M. D., A. V. DRITS, M. E. CLARKE, AND S. PLOURDE. 1998. Differential dormancy of co-occurring copepods. Deep-Sea Res. II **45:** 1709–1740, doi:10.1016/S0967-0645(98)80014-3

OLIVIERI, R. A., AND F. P. CHAVEZ. 2000. A model of plankton dynamics for the coastal upwelling system of Monterey Bay, California. Deep-Sea Res. II **47:** 1077–1106, doi:10.1016/S0967-0645(99)00137-X

OSBORN, D. A., M. W. SILVER, C. G. CASTRO, S. M. BROS, AND F. P. CHAVEZ. 2007. The habitat of mesopelagic scyphomedusae in Monterey Bay, California. Deep-Sea Res. I **54:** 1241–1255, doi:10.1016/j.dsr.2007.04.015

PENNINGTON, J. T., AND F. P. CHAVEZ. 2000. Seasonal fluctuations of temperature, salinity, nitrate, chlorophyll and primary production at station H3/M1 over 1989–1996 in Monterey Bay, California. Deep-Sea Res. II **47:** 947–973, doi:10.1016/S0967-0645(99)00132-0

PRELL, W., A. MARTIN, J. CULLEN, AND M. TREND. 1999. The Brown University Foraminiferal Data Base. IGBP PAGES/World Data Center-A for Paleoclimatology, Data Contribution Series #1999-027. The Brown University Foraminiferal Data Base. NOAA/NGDC Paleoclimatology Program, Boulder [Internet]. Available from http://www.ncdc.noaa.gov/paleo/datalist.html

RASKOFF, K. A. 2001. The impact of El Niño events on populations of mesopelagic hydromedusae. Hydrobiologia **451:** 121–129, doi:10.1023/A:1011812812662

RHUMBLER, L. 1911. Die Foraminiferen (Thalamophoren) der Plankton-Expedition, Teil 1. Die allgemeinen Organisationsverhältnisse der Foraminiferen. Lipsius & Tischer, [The Foraminifera (Thalamophoren) of the Plankton Expedition, Part 1. The general organizational relationships of foraminifera.]

ROBISON, B. H. 1992. Midwater research methods with MBARI's ROV. Mar. Technol. Soc. J. **26:** 32–39.

———. 2004. Deep pelagic biology. J. Exp. Mar. Biol. Ecol. **300:** 253–272, doi:10.1016/j.jembe.2004.01.012

———. 2009. Conservation of deep pelagic biodiversity. Conserv. Biol. **23:** 847–858, doi:10.1111/j.1523-1739.2009.01219.x

———, K. R. REISENBICHLER, AND R. E. SHERLOCK. 2005. Giant larvacean houses: Rapid carbon transport to the deep sea floor. Science **308:** 1609–1611, doi:10.1126/science.1109104

———, ———, ———, J. M. B. SILGUERO, AND F. P. CHAVEZ. 1998. Seasonal abundance of the siphonophore, *Nanomia bijuga*, in Monterey Bay. Deep-Sea Res. II **45:** 1741–1751, doi:10.1016/S0967-0645(98)80015-5

SALTZMAN, J., AND K. F. WISHNER. 1997a. Zooplankton ecology in the eastern tropical Pacific oxygen minimum zone above a seamount: 1. General trends. Deep-Sea Res. I **44:** 907–930, doi:10.1016/S0967-0637(97)00007-1

———, AND ———. 1997b. Zooplankton ecology in the eastern tropical Pacific oxygen minimum zone above a seamount: 2. Vertical distribution of copepods. Deep-Sea Res. I **44:** 931–954, doi:10.1016/S0967-0637(97)00006-X

SAUTTER, L. R., AND R. C. THUNELL. 1991. Planktonic foraminiferal response to upwelling and seasonal hydrographic conditions—sediment trap results from San-Pedro-Basin, Southern California Bight. J. Foraminifer. Res. **21:** 347–363, doi:10.2113/gsjfr.21.4.347

SCHLINING, B. 1999. Seasonal intrusions of equatorial waters in Monterey Bay and their effects on mesopelagic animal distributions. Moss Landing Marine Laboratories.

SILGUERO, J. M. B., AND B. H. ROBISON. 2000. Seasonal abundance and vertical distribution of mesopelagic calycophoran siphonophores in Monterey Bay, CA. J. Plankton Res. **22:** 1139–1153, doi:10.1093/plankt/22.6.1139

SPINDLER, M., O. R. ANDERSON, C. HEMLEBEN, AND A. W. H. BÉ. 1978. Light and electron microscopic observations of gametogenesis in *Hastigerina pelagica* (Foraminifera). J. Protozool. **25:** 427–433.

———, C. HEMLEBEN, U. BAYER, A. W. H. BE, AND O. R. ANDERSON. 1979. Lunar periodicity of reproduction in the planktonic foraminifer *Hastigerina pelagica*. Mar. Ecol. Prog. Ser. **1:** 61–64, doi:10.3354/meps001061

———, ———, J. B. SALOMONS, AND L. P. SMIT. 1984. Feeding behavior of some planktonic foraminifers in laboratory cultures. J. Foraminifer. Res. **14:** 237–249, doi:10.2113/gsjfr.14.4.237

SPRAGUE, G. F., AND S. C. WINANS. 2006. Eukaryotes learn how to count: Quorum sensing by yeast. Genes Dev. **20:** 1045–1049, doi:10.1101/gad.1432906

SUGIHARA, G., M. CASDAGLI, E. HABJAN, D. HESS, P. DIXON, AND G. HOLLAND. 1999. Residual delay maps unveil global patterns of atmospheric nonlinearity and produce improved local forecasts. Proc. Natl. Acad. Sci. USA **96:** 14210–14215, doi:10.1073/pnas.96.25.14210

SWANBERG, N. R., AND D. A. CARON. 1991. Patterns of sarcodine feeding in epipelagic oceanic plankton. J. Plankton Res. **13:** 287–312, doi:10.1093/plankt/13.2.287

THUESEN, E. V., C. B. MILLER, AND J. J. CHILDRESS. 1998. Ecophysiological interpretation of oxygen consumption rates and enzymatic activities of deep-sea copepods. Mar. Ecol. Prog. Ser. **168:** 95–107, doi:10.3354/meps168095

VISSCHER, P. K. 2007. Group decision making in nest-site selection among social insects. Annu. Rev. Entomol. **52:** 255–275, doi:10.1146/annurev.ento.51.110104.151025