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Seasonality in Planktic Foraminifera of the Central California Coastal Upwelling Region

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Abstract

The association between planktic foraminiferal assemblages and local hydrography make foraminifera invaluable proxies for environmental conditions. Modern foraminiferal seasonality is important for interpreting fossil distributions and shell geochemistry as paleoclimate proxies. Understanding this seasonality in an active upwelling area is also critical for anticipating which species may be vulnerable to future changes in upwelling intensity and ocean acidification. Two years (2012-2014) of plankton tows, along with Conductivity-Temperature-Density profiles and carbonate chemistry measurements taken along the North-Central California shelf offer new insights into the seasonal dynamics of planktic foraminifera in a seasonal coastal upwelling regime. This study finds an upwelling-affinity for *Neogloboquadrina pachyderma* as well as a seasonal and upwelling associated alternation between dominance of *N. pachyderma* and *Neogloboquadrina incompta*, consistent with previous observations. *Globigerina bulloides*, however, shows a strong

affinity for non-upwelled waters, in contrast to findings in Southern California where the species is often associated with upwelling. We also find an apparent lunar periodicity in the abundances of all species and confirm the presence of foraminifera at very low saturation state of calcite.

1 Introduction

Planktic foraminifera have a long history as paleoceanographic proxies due to their environmental sensitivity, cosmopolitan distribution and extensive fossil record. The close association between planktic species and local hydrography means that fossil foraminiferal assemblages have often been used to reconstruct the movement of water masses through time (e.g. Berger, 1968; McIntyre et al., 1972; Oberhänsli et al., 1992; Ufkes et al., 1998). However, at sites where overlying water masses change seasonally, the foraminiferal fossil record will represent a combination of individuals that may have grown under vastly different conditions. This averaging of short-term variability has the potential to impact the interpretation of any proxy based on foraminifera. Seasonality in a variety of environments has been shown to have a pronounced effect on foraminiferal communities, with species assemblages changing throughout the year (Thunell et al., 1983; Reynolds and Thunell, 1985; Thunell and Honjo, 1987; Thunell and Sautter, 1992; Ortiz et al., 1995; Marchant et al., 1998; Eguchi et al., 2003). Previous studies have explored seasonal assemblage shifts in the North Pacific, including at Station Papa (Thunell and Reynolds, 1984; Reynolds & Thunell, 1985), in the California Current off of Oregon (>130 km offshore) (Ortiz & Mix, 1992), in Santa Barbara (Kincaid et al., 2000; Darling et al., 2003), Southern California (Sautter & Thunnell, 1991), and the Western Pacific (Eguchi et al., 2003). The majority of this work has focused on open-ocean assemblages, however, leaving a gap in understanding of seasonal dynamics in

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coastal upwelling regions, as well as a significant spatial gap within the California Current system between Southern California and Oregon.

An improved understanding of coastal upwelling fauna is also important for interpreting the paleoclimate record of these conditions (Reynolds and Thunell, 1986; Naidu and Malmgren, 1995; Vénec-Peyré and Caulet, 2000; Ishikawa and Oda, 2007). Many modern surveys have characterized upwelling-associated foraminifera through plankton tow and sediment trap studies in the tropics and sub-tropics (e.g. Thiede, 1975; Naidu, 1990; Thunell and Sautter, 1992; Pak et al., 2004; Salgueiro et al., 2008). Temperate and subpolar upwelling communities such as those found along the Central California shelf, however, remain poorly understood. On-shelf assemblages are particularly important for regions dominated by coastal upwelling processes where the alternation between upwelling and relaxation (periods of reduced wind-strength in between upwelling periods) has large regional impacts on oceanography and planktic communities (Botsford et al., 2006; Dugdale et al., 2006; Largier et al., 2006; Garcia-Reyes et al., 2014). From a paleontological perspective, nearshore assemblages are also of interest in the region as these are sediments most likely to contain a preserved carbonate fossil record due to their high sedimentation rates and the limitations of a narrow continental shelf above a shallow lysocline.

Understanding planktic foraminiferal assemblages in coastal upwelling regions is also relevant for predicting future climate and ecosystem perturbations. The California Current upwelling system is unusually susceptible to ocean acidification due to the incorporation of anthropogenic CO_2 into the surface ocean (Feely et al., 2008; Hofmann et al., 2010; Hauri et al., 2013). The pronounced influence of upwelling in this region is likely to intensify due to

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anthropogenic impacts (Bakun, 1990; Garcia-Reyes and Largier, 2012; Sydeman et al., 2014), compounding the impacts of ocean acidification. Planktic calcifiers such as pteropods (Bednaršek et al., 2014; Busch et al., 2014), coccolithophorids (Beaufort et al., 2011; Iglesias-Rodriguez et al., 2008; Langer et al., 2006), and foraminifera (Barker and Elderfield, 2002; Manno et al., 2012; Moy et al., 2009) may be especially vulnerable to reductions in ocean calcite and aragonite saturation state. Upwelled waters are already becoming more acidic along the California Margin, and the seasonal duration for which fauna are exposed to waters undersaturated with respect to aragonite is predicted to increase in the near future (Feely et al., 2008; Gruber et al., 2012; Harris et al., 2013; Hauri et al., 2013). The response of planktic foraminiferal assemblages to 20th century warming has been documented in Southern California (Field et al., 2006). An understanding of the modern seasonality of planktic foraminifera in this intense upwelling region can therefore serve as a baseline for future climate-driven change, and may help to identify which upwelling species may already be living at low pH, and potentially tolerant of low calcite-saturated waters that may resemble future conditions in the open ocean.

Here we focus on planktic foraminiferal assemblages sampled along a cross-shore transect over the Central California shelf extending from 1 km offshore to the shelf break (30-60 km offshore). Plankton tows, supported by *in situ* water column data and discrete bottle samples, allow a documentation of species associations based on instantaneous (as opposed to time-averaged) water column conditions. Our goal was to understand 1) the spatial and temporal distribution of planktic foraminifera along the Central California shelf and; 2) the manner in which species assemblages respond to high frequency changes in water mass, especially those associated with upwelling. These efforts may offer a general framework for interpreting seasonality in foraminiferal records drawn from analogous oceanographic regions, and could yield new insights into how this important group of marine calcifiers responds to ongoing climate change and acidification in coastal upwelling systems.

1.1 Regional Setting

The California Current is the southward flowing arm of the North Pacific Subtropical Gyre and along with the seasonal Davidson Countercurrent, flows adjacent to the Central Californian coastline to the west of our study sites. At many locations along the coast, wind-driven coastal upwelling brings deeper, colder, nutrient rich and low-O_2 water to the surface, with the strongest upwelling signal found in a 10 to 25 km band just offshore (Hickey and Guillery, 1979; Huyer, 1983; Lynn and Simpson, 1987).

At the latitudes of our study sites (37°– 39°N), wind-driven coastal upwelling is generally strongest in April-June (García-Reyes and Largier, 2012). During the upwelling season, wind-driven upwelling events are interspersed with relaxation periods, the combination of which is responsible for large changes in productivity in the plankton (Botsford et al., 2006; Dugdale et al., 2006; Largier et al., 2006; Garcia-Reyes et al., 2014). During the upwelling season, further complexity is introduced through the advection of upwelled water masses both away from the continent and alongshore, with water parcels in the region which are dominantly sourced from the north (Kaplan and Largier, 2006). Outside of the upwelling season (~September-March), upwelling events are generally absent and there is occasional occurrence of downwelling, with net northward flow of water. Advection rates are variable, but have been reported in the range of 10-30 km d^{-1} (Kaplan and Largier, 2006). This stable post-upwelling season generally lasts into December when the stability can be punctuated by storm conditions (Kaplan and Largier, 2006; García-Reyes and Largier, 2012). Together, these conditions create an environment of strong seasonality in terms of productivity,

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temperature, O_2, carbon chemistry and water mass, all of which would be expected to influence the species of planktic foraminifera present in the region.

2 Methods

2.1 Study Area

Plankton collection took place at 8 stations located at increasing distances from shore across the continental shelf (Fig. 1). Bodega Line (BL) (38°) sites start at nearshore station BL1, 1 km offshore, and extend across the shelf, to station BL5, 32 km offshore. These stations were sampled monthly to bimonthly from September 2012 to September 2014. Three additional stations were sampled in 2013 and 2014 as part of the Applied California Current Ecosystem Studies (ACCESS) cruises (three times per year), and are located just over the shelf break at 40-60 km offshore, spanning a latitudinal range from 37°– 39°N (Table 1). All sampling stations are shoreward of the central core of the California Current (Lynn & Simpson, 1987) and are strongly influenced by both spring/summer upwelling as well as winter storms (Fig. 1).

2.2 Sample Collection

Vertical net tows integrated foraminifera across the water column to a depth of 200 m or to 10 m above the sea floor at shallower sites. All foraminifera were sampled with a 150 µm mesh net. This approach potentially excludes very small juveniles, and therefore limited samples to foraminifera of an identifiable adult developmental stage. Most samples were placed in ambient surface seawater and kept chilled without further preservation to be picked immediately upon return to shore. When this was not feasible, samples were preserved shipboard in 95% ethanol, buffered to a pH > 8.5 with TRIS. Foraminifera were picked wet from bulk tow material, rinsed in DI water and archived in slides. All archived foraminifera were identified to the lowest possible taxonomic level. No distinction was made between living and dead individuals although almost all shells still contained some cytoplasm at the time of sorting. Taking into account the conservative end of the range of sinking rates for shells (e.g., 29-552 m day^{-1}; Takahashi and Be 1984) and that foraminifera were sampled from the upper 200m of the water column, we can assume that all foraminifera were likely alive within 6 days of collection. Transport data from the region allows us to further estimate a maximum horizontal transport of 50km in 5 days, indicating that all shells still within the water column were locally sourced (Kaplan & Largier, 2006).

2.3 Environmental Measurements

Water column profiles for temperature, salinity, dissolved O_2 (DO) and fluorescence were profiled across the plankton tow depths using a SeaBird conductivity-temperature-depth (CTD) sonde. Plankton tow nets were equipped with a flow meter for each cast; however, due to frequent failures, flow rates were unreliable and will not be reported here. At each station, discrete bottle samples of surface water and water from the bottom of each CTD cast were collected using a Niskin sampler. All water samples were analyzed spectrophotometrically for pH (total scale) using either a Sunburst SAMI (Submersible Autonomous Moored Instrument) modified for benchtop use (SD +/- 0.009) or an Ocean Optics Jaz Spectrophotometer EL200 (SD +/- 0.003) using *m*-cresol purple (Dickson *et al.* 2007). Total alkalinity was run via automated Gran titration on a Metrohm 809 Titrando (SD +/- 2.809 µmol/kg), with acid concentrations standardized to Dickson certified reference materials. Measurements of pH and alkalinity were carried out at UC Davis Bodega Marine Laboratory and used to characterize the entire inorganic carbon system, and calculate calcite saturation state (Ω_{Ca}) and [$CO_3^{=}$] using the software CO2Calc (Robbins et al., 2010). Thermocline depths were defined as the depth below 5m at which the greatest gradient in temperature occurred, exclusive of any temperature change with a slope of less than 0.1°C m^{-1}, in which case the thermocline was

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assumed to be deeper than the profiled water. Upwelling index is taken from the PFEL upwelling index modeled for 39°N (http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling.html), which is in general agreement with temperature measurements from the Bodega Ocean Observing Node (BL 1).

2.4 Data Analysis

For the four most abundant species, *G. bulloides, G. quinqueloba, N. incompta,* and *N. pachyderma,* we performed a PCA (Principle Components Analysis) on log-transformed counts. Potential explanatory variables included day of the lunar cycle relative to the new moon, upwelling index, duration of sustained upwelling as indicated by the PFEL upwelling index, surface and deep water carbonate system parameters, and CTD temperature, salinity, fluorescence, and DO. CTD data were binned into depths at 5m intervals to a depth of 25 m and then at 10m intervals. All variables were included in the initial analysis, but only variables with the highest loadings for each component with an eigenvalue greater than 1 were retained. Strongly interrelated or redundant parameters were manually excluded at this point in the analyses (i.e. a parameter explaining significant variance at multiple consecutive depths would have been considered at only one of these depths). A second PCA was performed on this subset of variables. Because each species was treated individually, although the initial variable set was the same in each case, the retained values varied across species. In addition, a regression matrix was used to indicate which, if any, environmental parameters correlated with each of the 4 four species abundances (Table 2; Supplemental).

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3 Methods

The assemblage was heavily dominated by the planktic species *N. pachyderma*, *N. incompta*, *G. quinqueloba* and *G. bulloides*, representing 35.3%, 23.1%, 13.5% and 11.7% of all recovered foraminifera, respectively. Less common forms included *Globigerinita glutinata*, *Globoquadrina hexagona, Globigerina calida*, *Globigerinita uvula* and *Globorotalia spp*., as well the occasional cosmopolitan species, *Orbulina universa* and subtropical *Neogloboquadrina dutertrei* and, rarely, benthic species of foraminifera. The presence of these latter taxa was sporadic and in low abundance (all <1% of the overall recovered foraminifera, with the exception of *G. glutinata* at 2.1%); therefore, further analysis will be confined to the four most abundant species.

At offshore stations BL3, BL4 and BL5 and off-shelf stations A2W, A4W and A6W, foraminifera displayed a clear seasonality. The year can be divided between Spring/Summer and Fall/Winter faunas that coincide with the upwelling-dominated and non-upwelling season (Fig. 2). Beginning in May, shortly after the onset of upwelling, samples began to show a high abundance of *G. quinqueloba.* A bloom of *N. pachyderma* occurs in June or July, after several months of sustained upwelling, followed by a decrease in abundance to less than 50% by the end of summer (Fig 2). *N. pachyderma* were also present through much of the winter in lower numbers in 2012-2013. By contrast, this species was virtually absent in the winter of 2013-2014, before reappearing after a period of sustained upwelling in July 2014 (Fig 2). In both years, the earliest *N. pachyderma* blooms appeared to initiate farther offshore, although abundances within a given samples did not appear to be directly linked to specific upwelling events.

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Following the end of the summer season, the Fall-Winter fauna shows a more even distribution of species and a distinct shift in the ratio of *N. pachyderma* to *N. incompta* (Fig 2). *N. incompta* was equally or more abundant than *N. pachyderma* during the non-upwelling season although it was present year-round. *G. bulloides* also began to appear in the water column in the fall, strongly associated with non-upwelled waters, and is present throughout the winters. *G. bulloides* was present primarily in the winter and either absent or found only in very low numbers during the summer season.

The same suite of species was present at nearshore stations BL1 and BL2, however, counts were lower year-round and most seasonal patterns seen offshore were not evident. *N. pachyderma* did appear to bloom during the summer at these stations, but remained in low abundance along with *N. incompta* year-round (Fig 3). *G. quinqueloba* was also observed year-round at these nearshore stations. A greater proportional abundance of *G. bulloides* was seen during the fall and winter at nearshore sites, consistent with findings at the offshore stations (Fig 3).

3.1 Environmental Measurements

CTD profiles and inorganic carbon system measurements carried out alongside plankton tows confirm the broad hydrographic trends in the region. In spring and summer, surface conditions were highly variable, reflecting the alternation between upwelling events and relaxation periods. Frequent changes in thermocline depth were observed, as well as intermittent blooms of near-surface productivity (Fig. 4). The result is a more surface-stratified and productive water column, with a shallow thermocline and high fluorescence in the upper water-column. During upwelling-season, near-surface temperatures cool to 8-9°C, and sub-surface waters approach calcite undersaturation (Ω_{Ca}<1), and display low DO (<4 mg/L at <90 m) (Fig 4).

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Despite consistently lower sub-surface DO and pH, high near-surface productivity often increased DO and pH near-surface values, creating a noticeable down-profile gradient in these parameters.

Beginning in the late fall, and continuing into early spring, a consistently deep thermocline was observed at all stations. This trend often had the effect of confining the entire on-shelf water column (including all tow samples) to this deep mixed layer, which dominated the shelf in winter. Temperatures were generally warmer (11-14°C) than during the upwelling season with relatively low fluorescence in the upper water column (<4) (Fig. 4) and surface pH around 8. Garcia-Reyes and Largier (2012) describe storm conditions, which are likely to have contributed to the deep mixed layer, observed outside of upwelling season, especially between January-March.

3.2 Principle Component Analysis

Because of the natural covariance of many of our environmental variables and the poor explanatory value of any pairwise correlation, PCA offers an informative way to distinguish the combined environmental conditions that are conducive to high abundance for a particular species. Over 92% of the variance in abundance of three out of these four species was explained by a given species' first principal component (Fig. 5). PC1 for *G. bulloides* was heavily loaded towards factors indicative of upwelling, including near-surface DO and [$CO_3^{=}$], and upper water column temperature (<40m), with fluorescence (reflecting primary productivity) loading onto PC2. For *G. quinqueloba,* both shallow and deep carbon system parameters as well as water column temperatures loaded onto PC1, with fluorescence again loading onto PC2. *N. pachyderma* showed a similar association, with carbon system parameters loading onto PC1, with temperature and DO on PC2 as well as lunar day. *N.*

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incompta was the only species for which PC1 explained less than 94% of its variance in abundance. Here, salinity loaded onto PC1, and temperature in the upper water column on PC2 (Fig 5).

3.3 Neogloboquadrinid Coiling Direction

Coiling direction for Neogloboquadrinids is recognized as an empirical proxy for sea-surface temperature in the sedimentary record (Ericson, 1959; Bandy, 1960; Kennett, 1968; Bé & Tolderlund, 1971; Vella, 1974; Arikawa, 1983; Reynolds & Thunell, 1986). We tested whether the relationship is consistent on shorter timescales with mixed assemblages of *N. pachyderma* (primarily sinestral coiling) and *N. incompta* (primarily dextral coiling). A very weak linear correlation with surface temperature is observed, between the ratio of *N. pachyderma* to all *N. pachyderma* and *N. incompta* (r^2 = 0.09626; p-value = 0.02). Correlations improved deeper in the water column, with a weak but notable relationship at 40 m (r^2 = 0.3285; p-value < 0.001) (Fig 6).

4 Discussion

4.1 Foraminiferal Seasonality

A key finding of this study is the clear seasonality of the four most abundant species of planktic foraminifera at offshore stations along the Central California shelf. Our findings highlight the importance of seasonal-scale water column shifts in dictating foraminiferal species abundances, as well as suggest which species may be most vulnerable to ocean acidification in the region. It may also act as a guide to paleoceanographers in deciphering the specific species most likely to be recording seasonal signals along the shelf. *G. quinqueloba* appears to be associated mainly with the early summer months and the beginning of upwelling season as indicated by the PFEL Upwelling Index for the relevant study years. *N.*

pachyderma blooms in the late summer months following the onset of upwelling. The presence of *G. bulloides* is all but confined to the winter non-upwelling season while *N. incompta* is present in all seasons. The year-round presence of *N. incompta* combined with summer blooms in *N. pachyderma* creates the appearance of a seasonal switch in the relative abundances of the two Neogloboquadrinids (Fig 2). These trends are described in more detail for each of the four species below.

4.1.1 Neogloboquadrinids

The seasonal trade-off observed at offshore stations between *N. pachyderma* and *N. incompta* is in agreement with previous studies interpreting seasonality from the geochemistry of the two species. Sediment trap data from the Western North Pacific found that the $\delta^{18}O$ of both *N. incompta* and *G. bulloides* reflects winter sea-surface temperature while *N. pachyderma* reflects summer (Sagawa et al., 2013). Similarly, Mg/Ca ratios in recent fossils from the Norwegian Sea indicate that *N. pachyderma* is primarily a summer bloom species while *N. incompta* records winter conditions (Nyland et al., 2006). The close association between *G. bulloides* and *N. incompta* seen here has also been noted previously both in the water column and in coretop records (Reynolds and Thunell, 1986; Giraudeau, 1993; Ufkes et al., 1998).

The ratio of *N. pachyderma* to *N. incompta* (previously *N. pachyderma* var. sinistral and *N. pachyderma* var. dextral respectively) has long been recognized to be paleoceanographically significant in marine sediments, with *N. pachyderma* associated with subpolar water masses, *N. incompta* associated with sub-tropical to temperate waters, and the ratio between the two acting as a proxy for sea-surface temperature (Ericson, 1959; Bandy, 1960; Kennett, 1968; Bé & Tolderlund, 1971; Vella, 1974; Arikawa, 1983; Reynolds & Thunell, 1986). The relationship observed here between coiling direction of Neogloboquadrinids and temperature

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is weak, at best, at the surface. The relationship is slightly stronger at 40 m depth (Fig 6), with an equal ratio between *N. incompta* and *N. pachyderma* found around 10.5°C. This ratio can largely be explained by the year-round presence of *N. incompta*, punctuated by a bloom of *N. pachyderma* in the summer along with cooler temperatures, especially in the subsurface. These findings validate on short time-scales what has been seen to be empirically true over longer time-scales: *N. pachyderma* is found primarily in high latitude waters and when occurring in temperate regions mixed with *N. incompta*, whether in the water column or sediment, is suggestive of an incursion of these cooler, northern waters and not the direct impact of upwelled waters (<10°C conditions).

4.1.2 Globigerinoides bulloides

Globigerinoides bulloides has previously been associated with active upwelling in Southern California (Sautter & Thunell, 1991; Field et al., 2006) and the Arabian Sea (Peeters et al., 2002). Observations along the Central California shelf are in direct contrast to this, with *G. bulloides* observed to be far more abundant during the Fall/Winter relaxation and storm season (Fig 2). It is notable that in at least one previous study, *G. bulloides* has shown a bimodal abundance in Southern California, with one population of *G. bulloides* associated with winter, and another population with the spring-summer upwelling season (Sautter & Thunell, 1991). Furthermore, two distinct genotypes of *G. bulloides* have been identified in Southern California, one of which is present in winter samples and was previously recognized in "subpolar" regions (Darling et al., 2003). We interpret the *G. bulloides* observed along the Central California Coast as connected to this "subpolar"/winter population, accounting for the differences in seasonal abundance seen at our Northern site compared to Southern California.

4.1.3 Spatial Dynamics

Nearshore stations BL1 and BL2 are shoreward from the primary band of coastal upwelling (Huyer, 1983) and show significantly less seasonality in species abundances with the exception of *G. bulloides,* which is more abundant in the fall and winter nearshore as well as offshore. Although non-spinose forms are also occasionally present at both nearshore sites, they do not show the seasonality that they do at offshore sites (Fig 3). Some of the differences seen in the fauna at BL1 and BL2 compared to offshore stations may be due to shallower tow depths at these sites (25 m and 45 m, respectively), and therefore a bias in favor of species living closer to the surface, which may include *G. bulloides*. However, shallow tows conducted at BL4 and BL5 confirm that all four species considered here are present in the upper water column (<30 m) at these sites, so depth alone cannot completely account for the nearshore/offshore difference in foraminiferal abundances. Nearshore stations may be sheltered from larger-scale transitions in source water that happen over most of the shelf, and more impacted by terrestrial processes.

Short-term spatial dynamics were also observed to impact foraminifera abundances. On days when overall productivity was low, abundances of all foraminifera species were relatively higher at sites with higher fluorescence (indicating higher primary productivity). Especially low fluorescence (near-surface fluorescence <2) was observed on collection days 2/4/2013, 1/16/2014, 7/1/2014 and 2/26/2013. On these days, foraminifera were recovered in much greater numbers at stations associated with peak fluorescence regardless of where along the transect the station was located (Fig 7). On 1/16/2014 no foraminifera were recovered at very low productivity stations BL1, BL5 or on 7/1/2014 at BL1, while other sites yielded >100 individuals. On 2/4/2013, BL2 was associated with the only observation of surface fluorescence >10 and yielded more foraminifera than all other sites combined. Fluorescence was low at all sites on 2/26/2013 and no foraminifera were recovered from these tows (Fig 7). These data indicate that phytoplankton productivity may ultimately be a limiting factor for all species. On days with higher measured fluorescence (productivity), the dominant spatial trend was towards higher abundances further offshore regardless of where peak productivity was observed.

4.1.4 Foraminifera in Reduced pH Waters

Upwelling-associated waters with low Ω_{Ca} were observed on multiple occasions during plankton tows. For an organism widely thought to be susceptible to ocean acidification (i.e. Barker and Elderfield, 2002; Manno et al., 2012; Moy et al., 2009; Orr et al., 2005), the association of multiple species of foraminifera already living at $\Omega_{Ca} < 1$ or very low Ω_{Ca} (<1.5) waters is notable. In particular, more than a quarter (26%) of all observed *N. pachyderma*, with its strong upwelling association, were found to occur in a water column with $\Omega_{Ca} < 1$ in the upper 160m. Culture studies with this species have indicated a decrease in shell weight associated with low Ω_{Ca} well within the range of those that *N. pachyderma* was found in during upwelling season, indicating the potential to impact carbonate flux in areas where this is an important calcifier (Manno et al., 2012). If *N. pachyderma* is already living near its Ω_{Ca} tolerance, this species may be exceptionally vulnerable to a continued increase in ocean acidification in this region. Conversely, upwelling-adapted *N. pachyderma* may prove to be an example of a calcifying plankton able to tolerate undersaturated waters.

4.2 Causes of Seasonality and Fluctuations in Abundance

One important mechanism contributing to the seasonal progression of foraminifera species along the shelf in Central California is the alternation between the direction of net water transport between upwelling and non-upwelling seasons. This phenomenon would account for

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the occurrence of *G. bulloides* in greater numbers outside of upwelling season when net poleward water transport is expected (Kaplan and Largier, 2006). Similarly, the influx of subpolar associated *N. pachyderma* could be due to this species being carried into the region during the southward transport of water that occurs during upwelling season (Kaplan and Largier, 2006). An alternation between the foraminiferal fauna of source waters additionally offers an explanation for the seasonal absence and reappearance of these two species. *N. incompta,* found year-round in the study region, may be present in both water masses.

In addition to the broad oscillation of source waters, higher counts of each species are associated with some specific water column characteristics. In most cases, species abundances could not be linked directly to single environmental parameters with much predictive power, but rather a suite of hydrographic and temporal variables were required to account for faunal assemblages. Attempts to model transformed species counts against measured parameters returned poor predictive values (Table 2). For some species, particular variables can be identified through pairwise correlation as having a significant effect on abundance. In *G. bulloides*, higher abundance correlates with higher water temperatures throughout the water column (Table 2). In *N. pachyderma*, higher abundances are associated with higher fluorescence, and thus enhanced primary production. For *N. incompta,* counts seem to loosely correlate with higher O_2 and lower salinities, while *G. quinqueloba* is not clearly correlated with any single measured parameter (Table 2).

PCAs for *G. bulloides, G. quinqueloba,* and *N. pachyderma* all show a high degree of variance explained by PC1 with loadings on carbon system parameters, temperature and DO, all parameters dependent on coastal upwelling conditions (Fig 5). However, the directions of those associations vary. *N. pachyderma,* and to a lesser extent, *G. quinqueloba,* seem to be associated with upwelling-like water conditions. Sediment trap time series have previously linked *G. quinqueloba* to productivity in the North Atlantic (Chapman, 2010), which would explain the association of this species with the high near-surface fluorescence and low sub-surface DO that immediately follow the onset of upwelling. *G. bulloides*, however, is negatively associated with upwelling-like water conditions, and more associated with warmer waters seen outside of upwelling season. In *N. incompta,* neither PC1 nor PC2 are loaded with parameters indicative of seasonal upwelling, and the relevant parameters seem to span the gambit of variables measured, including temperature, salinity, fluorescence and DO. This outcome is supported by untransformed counts, which indicate that this species is the only one clearly present at the tow sites year-round.

4.2.1 Lunar Periodicity

Abundances of *G. bulloides, G. quinqueloba, N. incompta* and *N. pachyderma* all display an abundance cycle with a 28 day period that appears to coincide with the lunar cycle (Fig. 8). Peak counts for each species occur within 7 days of the full moon, before dropping off before the new moon (Fig 8). This trend offers further evidence that planktic foraminifera reproduce on a lunar cycle (Spindler et al., 1979; Bijma et al., 1990; Bijma et al., 1994; Schiebel et al., 1997; Jonkers et al., 2014). The peak abundance for *G. bulloides* occurs before that in the other species, starting 3 days before the full moon and remaining high until 4 days after the full moon. Abundances in *N. pachyderma* and *N. incompta* begin to increase around the same time, but high abundances in these species continue until 5 and 7 days after the full moon respectively. Whether the observed offsets in peak abundance around the full moon represent inter-species differences in reproductive timing or are an artifact of sampling against a background of strong seasonality in a highly variable environment cannot be resolved from this dataset.

4.3 Application to the Fossil Record

The presence of seasonally distinct faunas along the Central California margin can be used in increasing the resolution of paleoceanographic and paleoecologic records, as different species clearly represent different states of the seasonal upwelling regime. Single-species geochemical records are likely to show a strong bias towards either upwelled or non-upwelled water masses, and therefore, could potentially be harnessed as a record of changes in upwelling intensity and associated water chemistry. Our findings reaffirm a strong relationship between the dominance of *N. pachyderma* in conditions favorable to upwelling. This pattern has been noted along the African margin (Giraudeau, 1993). As our record is based on discrete tows and not a continuous record, the percent composition of species cannot be directly translated into a sediment flux or to what would be preserved in aggregate in the fossil record. However, the summer bloom of *N. pachyderma* seen here is strong enough that this signal would likely dominate the annual assemblages, although the vast majority of *N. pachyderma* (81% of those seen in tows) occur between July and November.

Globigerinoides bulloides has been associated with upwelling at other sites globally (Sautter & Thunell, 1991; Peeters et al., 2002; Field et al., 2006) and even used as an upwelling indicator in the fossil record (Naidu, 1990; Kroon et al., 1991; Anderson & Prell, 1993; Naidu & Malmgren, 1996). However, within our study region, this species was present almost exclusively outside of upwelling season. 88% of the *G. bulloides* seen in our samples were observed between November and February. PCA supports these observations in indicating that the species is negatively associated with upwelling-like conditions in the region. This situation contrasts with findings in Southern California and the Oman Margin (Peeters et al., 2002; Field et al., 2006), highlighting the importance of using regionally specific associations where possible when interpreting planktic assemblages in the sediment record.

5 Conclusions

Surveys of planktic foraminifera retrieved from plankton tows both confirm and contradict findings of studies in analogous regions. Along the Central California shelf there is a clear association between upwelling and high abundances of *N. pachyderma,* which experience a summer bloom, as seen at other northern sites. This summer population of *N. pachyderma* appears to routinely experience low Ω_{Ca} waters, conditions that are predicted to increase in the near future. The *N. pachyderma* associated with upwelling and low temperatures are also reflected in the empirical relationship between *Neogloboquadrinid* coiling direction, seen previously in the sediment record, with a switch in dominance between *N. incompta* and *N. pachyderma* around 10.5°. *G. bulloides*, however, is associated in our study with non-upwelled waters, in contrast with populations found in Southern California and other upwelling regions. All species showed a lunar periodicity in their abundances, evidence of lunar timed reproduction. This study highlights the great wealth of information on seasonal-scale processes that is contained within foraminiferal shells. To access this information, it is however, of great importance to ground interpretations of foraminiferal proxies in species and regional ecology to the greatest extent possible.

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References

Anderson, D. M., and Prell, W. L.: A 300 kyr record of upwelling off Oman during the late Quaternary: evidence of the Asian southwest monsoon, Paleoceanography, 8(2), 193-208, 1993.

Arikawa, R.: Distribution and Taxonomy of Globigerina pachyderma (Ehrenberg) off the Sanriku Coast, Northeast Honshu, Japan: The science reports of the Tohoku University, Geology, 53(2), 103-A120, 1983.

Bakun, A.: Global Climate Change and Intensification of Coastal Ocean Upwelling, Science, 247(4939), 198-201, 1990.

Barker, S., and Elderfield, H.: Foraminiferal calcification response to glacial-interglacial changes in atmospheric CO2, Science, 297(5582), 833-836, 2002.

Beaufort, L., Probert, I., de Garidel-Thoron, T., Bendif, E., Ruiz-Pino, D., Metzl, N., Goyet, C., Buchet, N., Coupel, P., and Grelaud, M.: Sensitivity of coccolithophores to carbonate chemistry and ocean acidification, Nature, 476(7358), 80-83, 2011.

Bednaršek, N., Feely, R., Reum, J., Peterson, B., Menkel, J., Alin, S., and Hales, B.: Limacina helicina shell dissolution as an indicator of declining habitat suitability owing to ocean acidification in the California Current Ecosystem, Proc R Soc Lond B, 281(1785), 20140123, 2014.

Bandy, O. L.: The geologic significance of coiling ratios in the foraminifer Globigerina pachyderma (Ehrenberg) [California], J Paleontol, 34(4), 671-681, 1960.

Bé, A., and Tolderlund, D.: Distribution and ecology of living planktonic foraminifera in surface waters of the Atlantic and Indian Oceans, The micropaleontology of oceans, p. 105-149, 1971.

Berger, W. H.: Planktonic Foraminifera: selective solution and paleoclimatic interpretation, Deep Sea Res Oceanogr App, 15(1), 31-43, 1968.

Bijma, J., Erez, J., and Hemleben, C.: Lunar and semi-lunar reproductive cycles in some spinose planktonic foraminifers, J Foramin Res, 20(2), 117-127, 1990.

Bijma, J., Hemleben, C., and Wellnitz, K.: Lunar-influenced carbonate flux of the planktic foraminifer Globigerinoides sacculifer (Brady) from the central Red Sea, Deep Sea Res Pt 1, (41)3, 511-530, 1994.

Bijma, J., Hönisch, B., and Zeebe, R. E.: Impact of the ocean carbonate chemistry on living foraminiferal shell weight: Comment on "Carbonate ion concentration in glacial-age deep waters of the Caribbean Sea" by W. S. Broecker and E. Clark: Geochem Geophy Geosy, 3(11), 1064, 2002.

Botsford, L. W., Lawrence, C. A., Dever, E. P., Hastings, A., and Largier, J.: Effects of variable winds on biological productivity on continental shelves in coastal upwelling systems, Deep Sea Res Pt 2, 53(25), 3116-3140, 2006.

Busch, D. S., Maher, M., Thibodeau, P., and McElhany, P.; Shell Condition and Survival of Puget Sound Pteropods Are Impaired by Ocean Acidification Conditions, PLoS ONE, doi: 10.1371/journal.pone.0105884, 2014.

Chapman, M. R.: Seasonal production patterns of planktonic foraminifera in the NE Atlantic Ocean, Implications for paleotemperature and hydrographic reconstructions. Paleoceanography, 25(1), 2010.

Darling, K. F., Kucera, M., Wade, C. M., von Langen, P., and Pak, D.: Seasonal distribution of genetic types of planktonic foraminifer morphospecies in the Santa Barbara

Channel and its paleoceanographic implications, Paleoceanography, 18(2), 1032, 2003.

Darling, K. F., Thomas, E., Kasemann, S. A., Seears, H. A., Smart, C. W., and Wade, C. M.: Surviving mass extinction by bridging the benthic/planktic divide, Proc Natl A Sci, 106(31), 12629-12633, 2009.

Dickson, A. G., Sabine, C. L., and Christian, J. R.: SOP 6b: Determination of the pH of sea water using the indicator dye m-cresol purple, Guide to best practices for ocean CO_2 measurements. 2007.

Dugdale, R. C., Wilkerson, F. P., Hogue, V. E., and Marchi, A.: Nutrient controls on new production in the Bodega Bay, California, coastal upwelling plume, Deep Sea Res Pt 2, 53(25), 3049-3062, 2006.

Eguchi, N. O., Ujiié, H., Kawahata, H., and Taira, A.,: Seasonal variations in planktonic foraminifera at three sediment traps in the Subarctic, Transition and Subtropical zones of the central North Pacific Ocean, Mar Micropaleontol, 48,(2), p. 149-163, 2003.

Erez, J., Almogi‐Labin, A., and Avraham, S.: On the life history of planktonic foraminifera: Lunar reproduction cycle in Globigerinoides sacculifer (Brady), Paleoceanography, 6(3), 295-306, 1991.

Ericson, D. B.,: Coiling Direction of Globigerina pachyderma as a Climatic Index, Science, 130(3369), 219-220, 1959.

Feely, R. A., Sabine, C. L., Hernandez-Ayon, J. M., Ianson, D., and Hales, B.: Evidence for Upwelling of Corrosive "Acidified" Water onto the Continental Shelf, Science, 320(5882), 1490-1492, 2008.

Field, D. B., Baumgartner, T. R., Charles, C. D., Ferreira-Bartrina, V., and Ohman, M. D.: Planktonic Foraminifera of the California Current Reflect 20th-Century Warming, Science, 311(5757), 63-66, 2006.

García-Reyes, M., Largier, J. L., and Sydeman, W. J.: Synoptic-scale upwelling indices and predictions of phyto-and zooplankton populations, Prog Oceanogr, 120, 177-188, 2014.

Giraudeau, J.: Planktonic foraminiferal assemblages in surface sediments from the southwest African continental margin, Mar Geol, 110(1), 47-62, 1993.

Gruber, N., Hauri, C., Lachkar, Z., Loher, D., Frölicher, T. L., and Plattner, G.-K.: Rapid Progression of Ocean Acidification in the California Current System, Science, 337(6091), 220-223, 2012.

Harris, K. E., DeGrandpre, M. D., and Hales, B.: Aragonite saturation state dynamics in a coastal upwelling zone, Geophy Res Lett, 40(11), 2720-2725, 2013.

Hauri, C., Gruber, N., Vogt, M., Doney, S. C., Feely, R. A., Lachkar, Z., Leinweber, A., McDonnell, A. M. P., Munnich, M., and Plattner, G. K.: Spatiotemporal variability and long-term trends of ocean acidification in the California Current System, Biogeosciences, 10(1), 193-216, 2013.

Hickey, B. M.: The California current system---hypotheses and facts, Prog Oceanogr, 8, 191-279, 1979.

Hofmann, G. E., Barry, J. P., Edmunds, P. J., Gates, R. D., Hutchins, D. A., Klinger, T., and Sewell, M. A.: The effect of ocean acidification on calcifying organisms in marine ecosystems: an organism-to-ecosystem perspective, Annu Rev Ecol Evol Sy, 41, 127-147, 2010.

Huyer, A.: Coastal upwelling in the California current system, Prog Oceanogr, 12(3), 259-284, 1983.

Iglesias-Rodriguez, M. D., Halloran, P. R., Rickaby, R. E., Hall, I. R., Colmenero-Hidalgo, E., Gittins, J. R., Green, D. R., Tyrrell, T., Gibbs, S. J., and von Dassow, P.: Phytoplankton calcification in a high-CO2 world, Science, 320(5874), 336-340, 2008.

Ishikawa, S., and Oda, M.: Reconstruction of Indian monsoon variability over the past 230,000 years: Planktic foraminiferal evidence from the NW Arabian Sea open-ocean upwelling area, Mar Micropaleontol, 63(4), 143-154, 2007.

Jonkers, L., Reynolds, C. E., Richey, J., and Hall, I. R.: Lunar periodicity in the shell flux of some planktonic foraminifera in the Gulf of Mexico, Biogeosciences, 11(12), 17187-17205, 2014.

Kaplan, D. M., and Largier, J.,: HF radar-derived origin and destination of surface waters off Bodega Bay, California, Deep Sea Res Pt 2, 53(25), 2906-2930, 2006..

Kennett, J. P.: Latitudinal Variation in Globigerina pachyderma (Ehrenberg) in Surface Sediments of the Southwest Pacific Ocean, Micropaleontol, 14(3), 305-318, 1968.

Kincaid, E., Thunell, R. C., Le, J., Lange, C. B., Weinheimer, A. L., and Reid, F. M. H.: Planktonic foraminiferal fluxes in the Santa Barbara Basin: response to seasonal and interannual hydrographic changes, Deep Sea Res Pt 2, 47(6), 1157-1176, 2000.

Kroon, D., Steens, T.N.F. and Troelstra, S.R.: Onset of monsoonal related upwelling in the western Arabian Sea as revealed by planktonic foraminifers. In: Prell, W.L., Niitsuma, N., Emeis, K.C. and Meters, P., Porceedings Scientific Results, ODP 117, College Station (Ocean Drilling Program), p. 257-264, 1991.

Langer, G., Geisen, M., Baumann, K. H., Kläs, J., Riebesell, U., Thoms, S., and Young, J. R.: Species-specific responses of calcifying algae to changing seawater carbonate chemistry, Geochem Geophy Geosy, 7(9), 2006.

Largier, J. L., Lawrence, C. A., Roughan, M., Kaplan, D. M., Dever, E. P., Dorman, C. E., Kudela, R.M., Bollens, S. M, Wilerson, F. P., Dugdale, R. C., Botsford, L. W., Garfield, N., Kuebel Cervantes, B. and Koračin, D.: WEST: A northern California study of the role of wind-driven transport in the productivity of coastal plankton communities, Deep Sea Res Pt 2, 53(25), 2833-2849, 2006.

Lynn, R. J., and Simpson, J. J.: The California Current system: The seasonal variability of its physical characteristics, J Geophys Res, 92, 12947-12966, 1987.

Manno, C., Morata, N., and Bellerby, R.: Effect of ocean acidification and temperature increase on the planktonic foraminifer Neogloboquadrina pachyderma (sinistral), Polar biol, 35(9), 1311-1319, 2012.

Marchant, M., Hebbeln, D., and Wefer, G.: Seasonal flux patterns of planktic foraminifera in the Peru–Chile current, Deep Sea Res Pt 1, 45(7), 1161-1185, 1998.

Marshall, B. J., Thunell, R. C., Henehan, M. J., Astor, Y., and Wejnert, K. E.: Planktonic foraminiferal area density as a proxy for carbonate ion concentration: A calibration study using the Cariaco Basin Ocean Time Series, Paleoceanography, 28(2), doi: 10.1002/palo.20034, 2013.

McIntyre, A., Ruddiman, W. F., and Jantzen, R.: Southward penetrations of the North Atlantic polar front: faunal and floral evidence of large-scale surface water mass movements over the last 225,000 years, Deep Sea Res Oceanogr App, 19(1), 61-77, 1972.

Biogeosciences Discuss., doi:10.5194/bg-2015-626, 2016
Manuscript under review for journal Biogeosciences
Published: 18 January 2016

Moy, A. D., Howard, W. R., Bray, S. G., and Trull, T. W.: Reduced calcification in modern Southern Ocean planktonic foraminifera, Nature Geosci, 2(4), 276-280. 2009.

Naidu, P.: Distribution of upwelling index planktonic foraminifera in the sediments of the western continental-margin of india, Oceanologica Acta, 13(3), 327-333, 1990.

Naidu, P. D., and Malmgren, B. A.: Monsoon upwelling effects on test size of some planktonic foraminiferal species from the Oman Margin, Arabian Sea: Paleoceanography, 10(1), 117-122, 1995.

Naidu, P. D., and Malmgren, B. A.: A high resolution record of late Quaternary upwelling along the Oman Margin, Arabian Sea based on planktonic foraminifera, Paleoceanography, 11(1), 129-140, 1996.

Nyland, B. F., Jansen, E., Elderfield, H., and Andersson, C.: Neogloboquadrina pachyderma (dex. and sin.) Mg/Ca and δ18O records from the Norwegian Sea, Geochem Geophys Geosy, 7(10), doi:10.1029/2005GC001055, 2006.

Oberhänsli, H., Bénier, C., Meinecke, G., Schmidt, H., Schneider, R., and Wefer, G.: Planktonic foraminifers as tracers of ocean currents in the eastern South Atlantic, Paleoceanography, 7(5), 607-632, 1992.

Orr, J. C., Fabry, V. J., Aumont, O., Bopp, L., Doney, S. C., Feely, R. A., Gnanadesikan, A., Gruber, N., Ishida, A., Joos, F., Key, R. M., Lindsay, K., Maier-Reimer, E., Matear, R., Monfray, P., Mouchet, A., Najjar, R. G., Plattner, G.-K., Rodgers, K. B., Sabine, C. L., Sarmiento, J. L., Schlitzer, R., Slater, R. D., Totterdell, I. J., Weirig, M.-F., Yamanaka, Y., and Yool, A.: Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms, Nature, 437(7059), 681-686, 2005.

Ortiz, J. D., Mix, A. C., and Collier, R. W.: Environmental control of living symbiotic and asymbiotic foraminifera of the California Current, Paleoceanography, 10(6), 987-1009, 1995.

Pak, D. K., Lea, D. W., and Kennett, J. P.: Seasonal and interannual variation in Santa Barbara Basin water temperatures observed in sediment trap foraminiferal Mg/Ca, Geochem Geophy Geosy, 5(12), doi:10.1029/2004GC000760, 2004.

Peeters, F. J. C., Brummer, G.-J. A., and Ganssen, G.: The effect of upwelling on the distribution and stable isotope composition of Globigerina bulloides and Globigerinoides ruber (planktic foraminifera) in modern surface waters of the NW Arabian Sea, Global Planet Change, 34(4), p. 269-291, 2002.

Reynolds, L., and Thunell, R. C.: Seasonal succession of planktonic foraminifera in the subpolar North Pacific, J Foramin Res, 15(4), 282-301, 1985.

Reynolds, L. A., and Thunell, R. C.: Seasonal production and morphologic variation of Neogloboquadrina pachyderma (Ehrenberg) in the northeast Pacific, Micropaleontology, 32(1), 1-18, 1986.

Robbins, L. L., Hansen, M.E., Kleypas, J.A., and Meylan, S.C.: CO2calc—A user-friendly seawater carbon calculator for Windows, Max OS X, and iOS (iPhone), U.S. Geological Survey Open-File Report, p. 2010–1280, 2010.

Russell, A. D., Hönisch, B., Spero, H. J., and Lea, D. W.: Effects of seawater carbonate ion concentration and temperature on shell U, Mg, and Sr in cultured planktonic foraminifera, Geochim Cosmochim Acta, 68(21), 4347-4361, 2004.

Sagawa, T., Kuroyanagi, A., Irino, T., Kuwae, M., and Kawahata, H.: Seasonal variations in planktonic foraminiferal flux and oxygen isotopic composition in the western North

Pacific: Implications for paleoceanographic reconstruction, Mar Micropaleontol, 100, 11-20, 2013.

Salgueiro, E., Voelker, A., Abrantes, F., Meggers, H., Pflaumann, U., Lončarić, N., González-Álvarez, R., Oliveira, P., Bartels-Jónsdóttir, H. B., Moreno, J., and Wefer, G.: Planktonic foraminifera from modern sediments reflect upwelling patterns off Iberia: Insights from a regional transfer function, Mar Micropaleontol, 66(4), 135-164, 2008.

Sautter, L. R., and Thunell, R. C.: Planktonic foraminiferal response to upwelling and seasonal hydrographic conditions; sediment trap results from San Pedro Basin, Southern California Bight, J Foramin Res, 21(4), 347-363, 1991.

Schiebel, R., Bijma, J., & Hemleben, C.: Population dynamics of the planktic foraminifer Globigerina bulloides from the eastern North Atlantic, Deep Sea Res Pt 1, 44(9), 1701-1713, 1997.

Schneider, C. A., Rasband, W. S., and Eliceiri, K. W.: NIH Image to ImageJ: 25 years of image analysis: Nat Meth, 9(7), 671-675, 2012.

Spindler, M., Hemleben, C., Bayer, U., Be, A. W. H. and Anderson, O.R.: Lunar Periodicity of Reproduction in the Planktonic Foraminifer Hastigerina pelagica, Mar Ecol Prog Ser, 1, 61-64, 1979.

Sydeman, W. J., García-Reyes, M., Schoeman, D. S., Rykaczewski, R. R., Thompson, S. A., Black, B. A., and Bograd, S. J.: Climate change and wind intensification in coastal upwelling ecosystems, Science, 345(6192), 77-80, 2014.

Takahashi, K., and Be, A. W. H.,: Planktonic foraminifera: factors controlling sinking speeds, Deep Sea Res, 31(12), 1477-1500., 1984.

Thiede, J.: Distribution of foraminifera in surface waters of a coastal upwelling area, Nature, 253(5494), 712-714, 1975.

Thunell, R., and Sautter, L. R.: Planktonic foraminiferal faunal and stable isotopic indices of upwelling: a sediment trap study in the San Pedro Basin, Southern California Bight, Geol Soc Lond, Special Publications, 64(1), 77-91, 1992.

Thunell, R. C., Curry, W. B., and Honjo, S.: Seasonal variation in the flux of planktonic foraminifera: time series sediment trap results from the Panama Basin, Earth Planet Sci Lett, 64(1), 44-55, 1983.

Thunell, R. C., and Honjo, S.: Seasonal and interannual changes in planktonic foraminiferal production in the North Pacific, Nature, 328(6128), 335-337, 1987.

Ufkes, E., Fred Jansen, J. H., and Brummer, G.-J. A.: Living planktonic foraminifera in the eastern South Atlantic during spring: Indicators of water masses, upwelling and the Congo (Zaire) River plume, Mar Micropaleontol, 33(1), 27-53, 1998.

Vella, P.: Coiling Ratios of Neogloboquadrina Pachyderma (Ehrenberg): Variations in Different Size Fractions, Geol Soc Am Bull, 85(9), 1421-1424, 1974.

Vénec-Peyré, M. T., and Caulet, J. P.: Paleoproductivity changes in the upwelling system of Socotra (Somali Basin, NW Indian Ocean) during the last 72,000 years: evidence from biological signatures, Mar Micropaleontol, 40(3), 321-344, 2000.

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Table 1. Station locations, depths and the number of times sampled over the course of this study.

Station	Lat	Long	Depth Sampled (m)	# Times Sampled
BL1	38° 16' 59"	-123° 04' 60"	25	15
BL2	38° 23' 38"	-123° 13' 00"	45	15
BL3	38° 21' 05"	-123° 14' 20"	90	15
BL4	38° 26' 20"	-123° 27' 01"	120	15
BL5	38° 21' 05"	-123° 37' 59"	200	14
A2W	38° 02' 45"	-123° 33' 47"	200	5
A4W	37° 52' 55"	-123° 28' 30"	200	4
A6W	37° 43' 20"	-123° 13' 59"	200	5

Table 2. Variables with a pairwise correlation with *G. bulloides*, *N. incompta,* or *N. pachyde*

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rma with a $R^2 > 0.4$

Species	Pairwise Correlated Variables	R2	p-values
# *G. bulloides*	Temp (40m), DO (40m), Temp (50m), Temp (60m), Temp (70m), Temp (80m), Salinity (80m), Temp (90m), Salinity (90m)	0.472607013, 0.415363192, 0.543006409, 0.534616821, 0.54615838, 0.532835148, -0.43100009, 0.551436524, -0.44262823	0.0001051, 0.0007877, <0.00005, <0.00005, <0.00005, <0.00005, 0.0004704, 3.40E-06, 0.0003154
# *N. pachyderma*	Fluorescence (Surface), Fluorescence (5), Fluorescence (30), Fluorescence (40), Fluorescence (50), Fluorescence (60), Fluorescence (70), Fluorescence (80), Fluorescence (90)	0.52290381, 0.433193966, 0.700259162, 0.756816474, 0.793529581, 0.737437062, 0.673743582, 0.66364351, 0.63463041	<0.00005, 0.0004367, <0.00005, <0.00005, <0.00005, <0.00005, <0.00005, <0.00005, <0.00005
# *N. incompta*	DO (30m), Salinity (30m), Salinity (40m), DO (50m), Salinity (50m), DO (60m), Salinity (60m), DO (70m), Salinity (70m), DO (80m), Salinity (80m), Salinity (90m)	0.480816644, -0.40322206, -0.47821834, 0.45855532, -0.459680386, 0.440141197, -0.481245826, 0.401425852, -0.479418468, 0.42139135, -0.5091728, -0.42370964	<0.00005, 0.001156, <0.00005, 0.0001781, 0.0001709, 0.0003439, <0.00005, 0.001222, <0.00005, 0.0006476, <0.00005, 0.0006001

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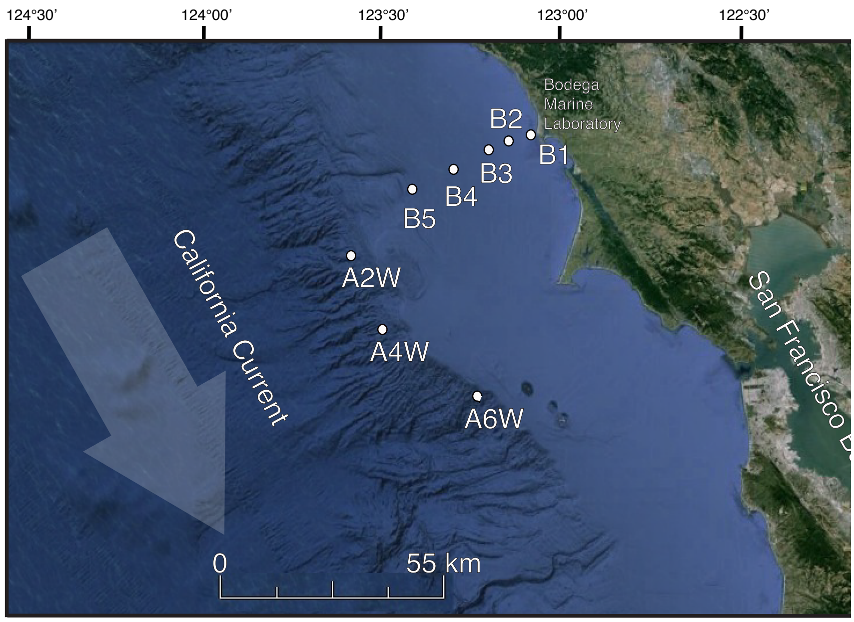

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3 Figure 1. Map of tow stations BL1-5, A2W, A4W and A6W.

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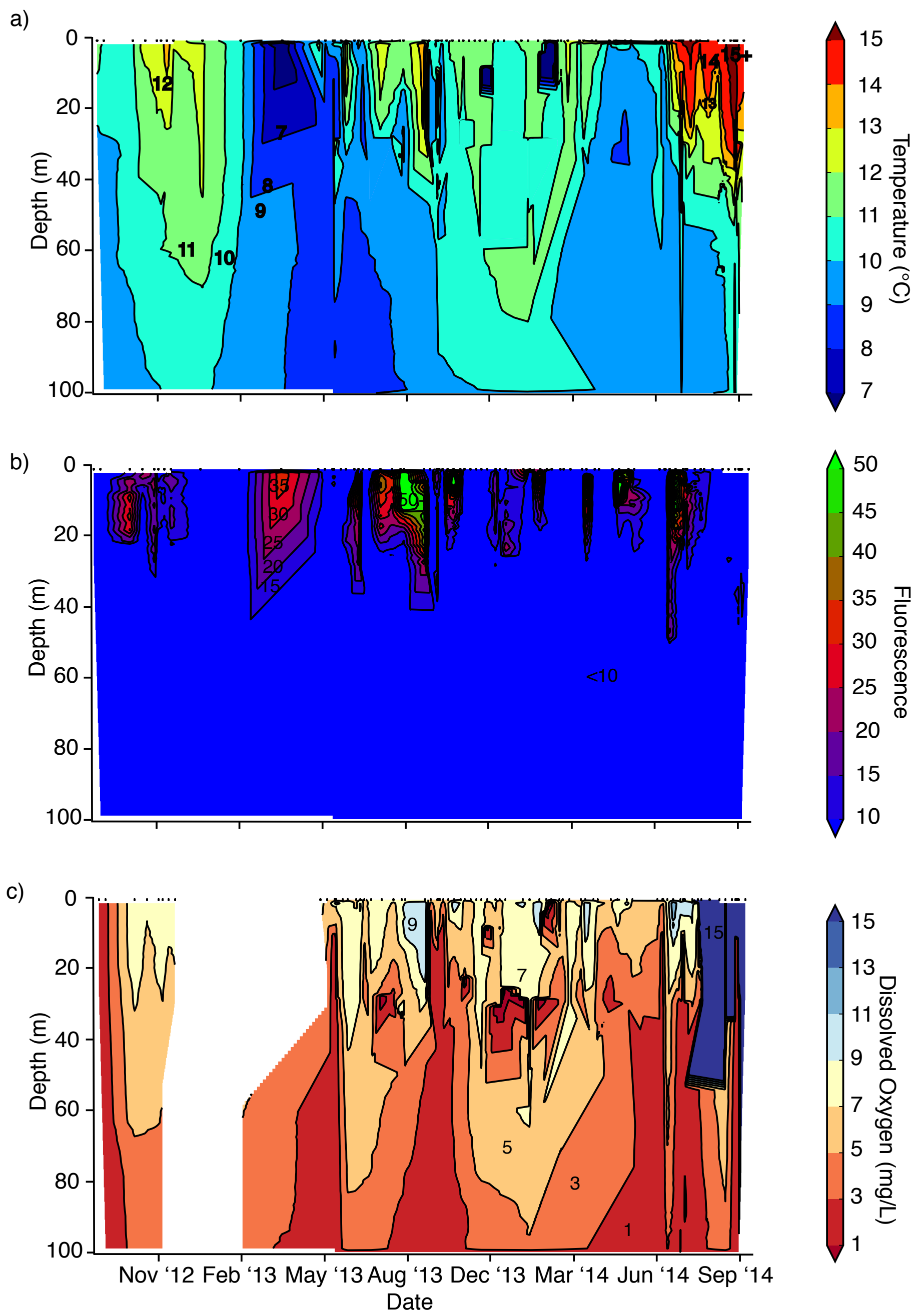

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2 Figure 2. A time-series of CTD cast profiles for a) temperature, b) productivity, and c) DO

3 taken between September 2012 and October 2014. Time-series are compiled from CTD casts

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at BL5 in conjunction with plankton tows and supplemented with data from weekly CTD casts taken at BL1 as a part of the Bodega Ocean Observing Node.

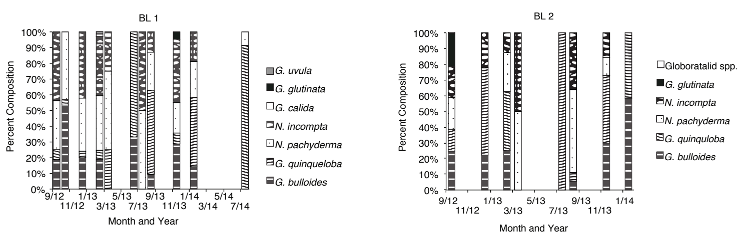

Figure 3. Relative abundance of all species at nearshore stations BL1 and BL2.

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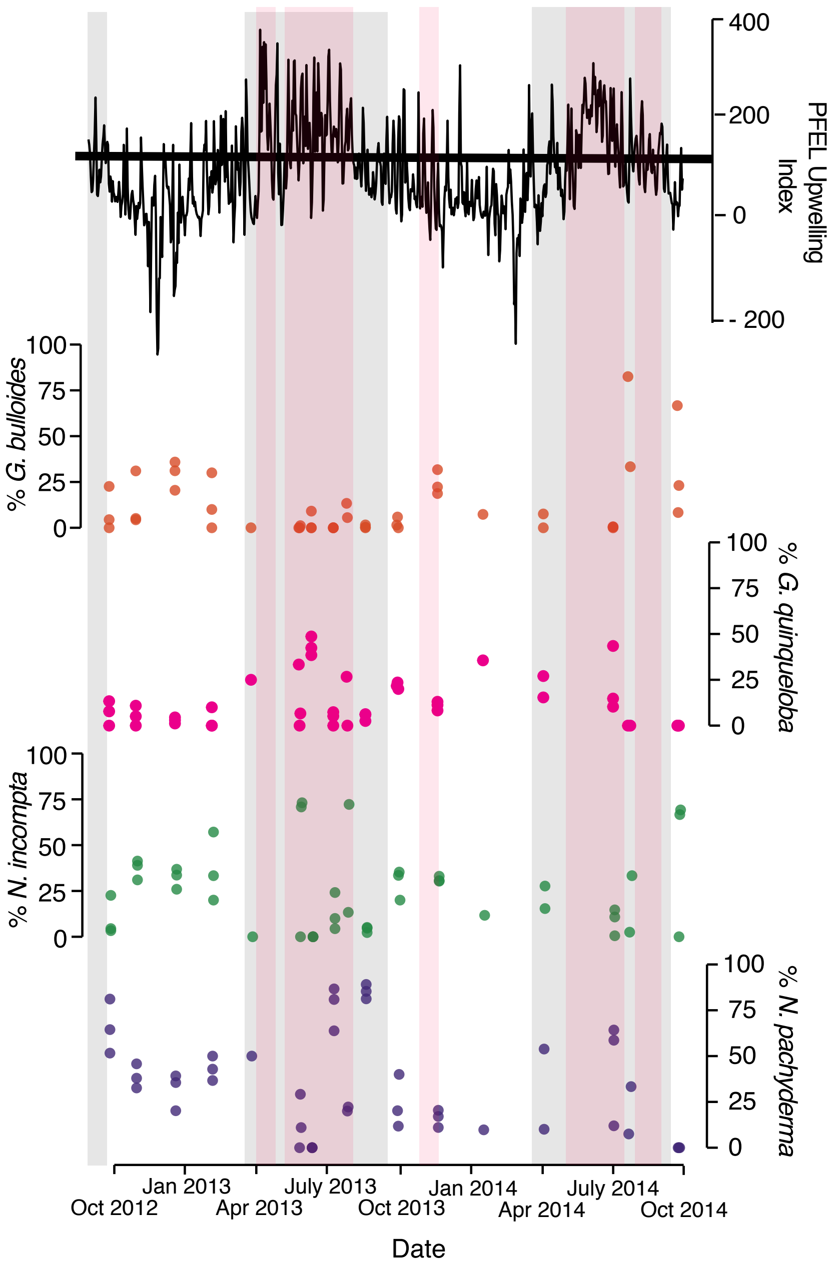

Figure 4. PFEL upwelling index for 39°N, with "upwelling season" shaded in gray, and periods of sustained upwelling conditions during the relevant years shaded in red. Percent abundances from vertical tows of *G. bulloides, G. quinqueloba*, *N. incompta,* and *N.*

pachyderma from offshore stations BL3, BL4, BL5 and off-shelf stations AW2, AW4, and AW6 shown in orange, pink, green and purple, respectively.

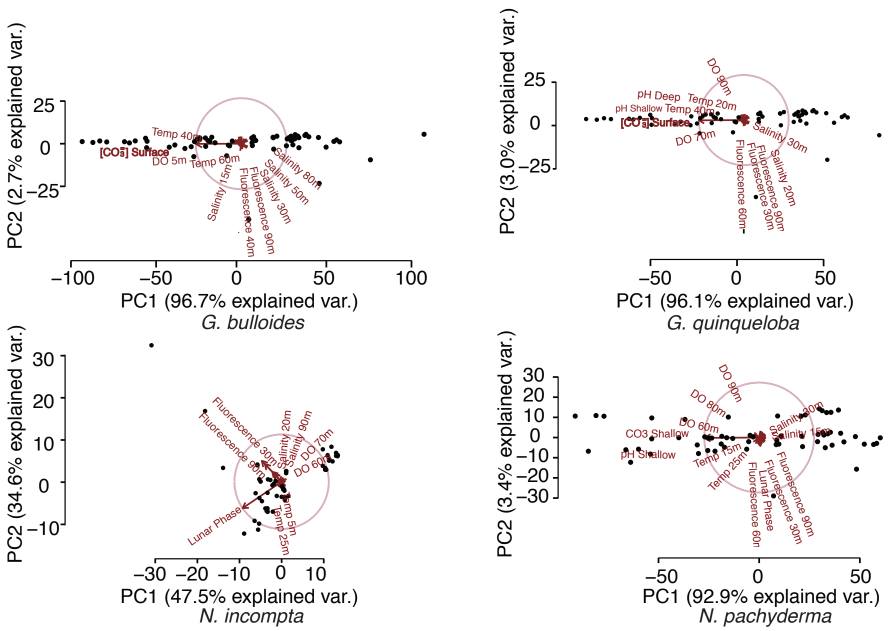

Figure 5. Biplots of Principle Components 1 and 2 for *G. bulloides, G. quinqueloba*, *N. incompta,* and *N. pachyderma.*

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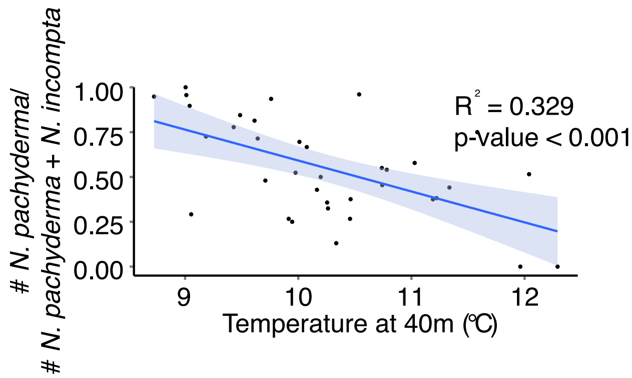

Ratio of *N. pachyderma* to *N. pachyderma* and *N. incompta* at 40m depth with 95% confidence envelopes.

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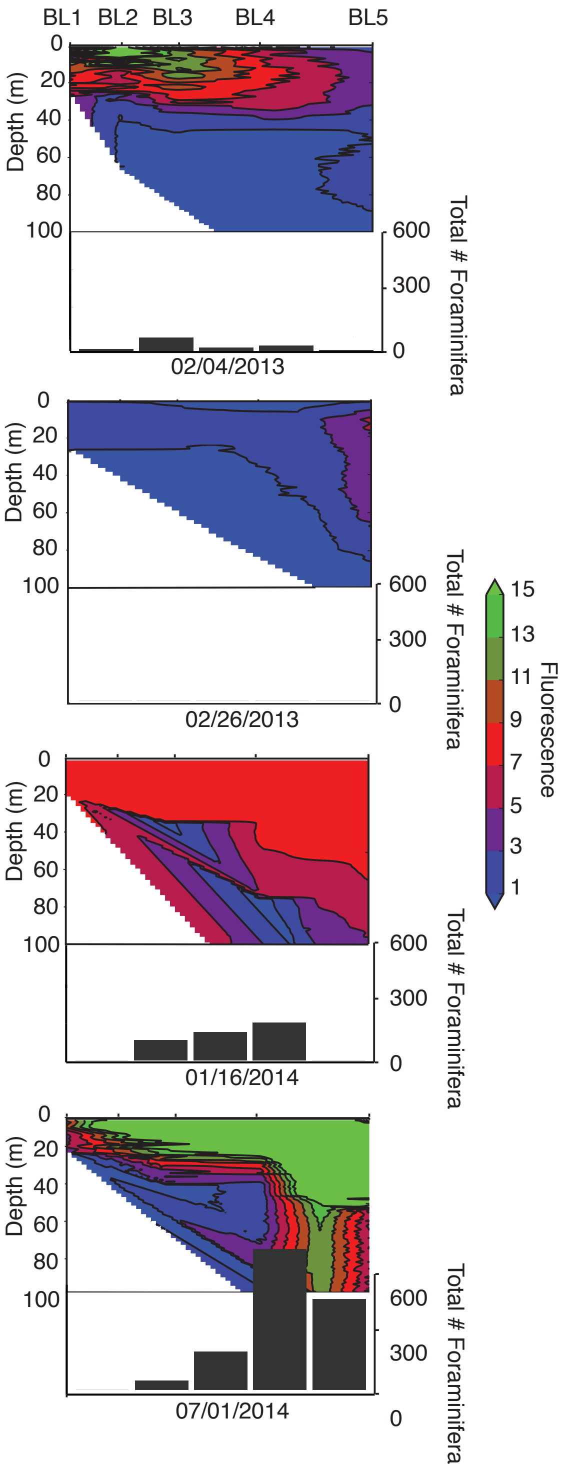

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Figure 7. Water column fluorescence data and total number of foraminifera recovered at stations BL 1-5 on four days of extremely low productivity. CTD data from these 5 stations demonstrates small-scale variability from 1 to 32 km offshore along the continental shelf, and compared this with the total number of foraminifera retrieved at each of these stations.

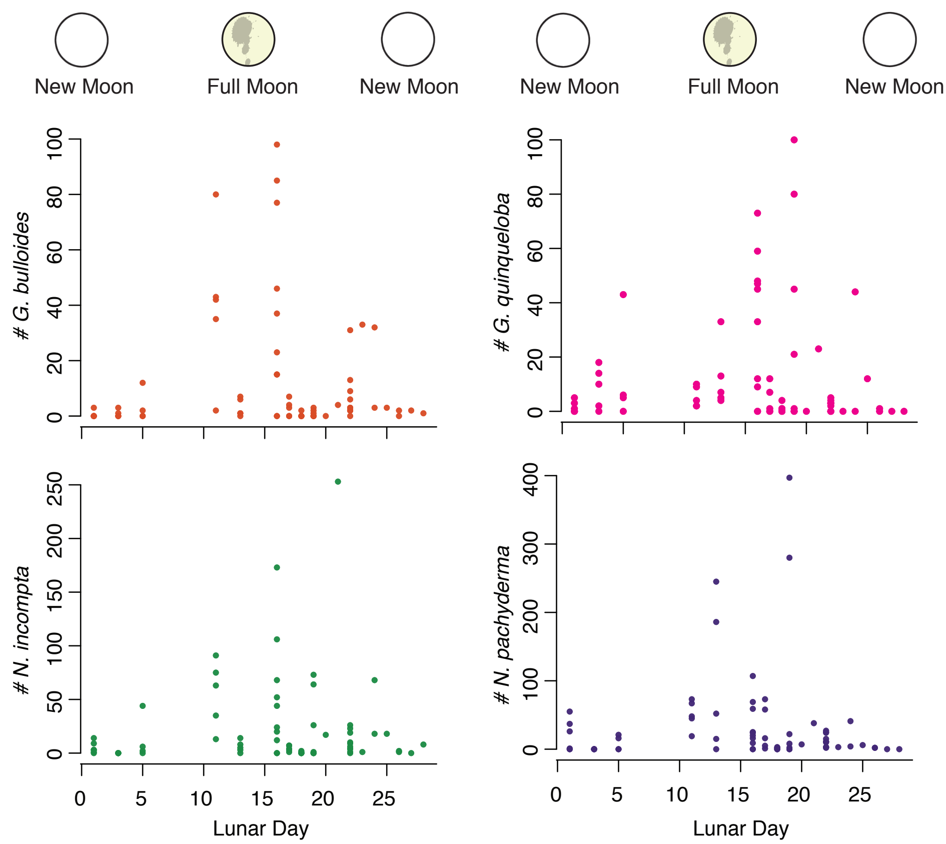

Figure 8. *G. bulloides, G. quinqueloba*, *N. incompta,* and *N. pachyderma* counts by lunar day from the new moon (Day 0) to Full Moon (Day ~14).