Seasonality in Planktic Foraminifera of the Central California Coastal Upwelling Region

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Abstract

The close 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 document the presence of foraminifera even 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 distribution 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; Pak et al., 2004). Previous studies have explored seasonal assemblage shifts in the North Pacific, including at Station Papa (50°N, 145°W; Thunell and Reynolds, 1984; Reynolds & Thunell, 1985), in the California Current off of Oregon (>130 km offshore) (Ortiz & Mix, 1992), in the Santa Barbara Basin (Kincaid et al., 2000; Darling et al., 2003), off Southern California (Sautter & Thunell, 1991), and in the Western Pacific (Eguchi et al., 2003). The majority of this prior work has focused on open-ocean assemblages, however, leaving a gap in understanding the seasonal dynamics in coastal upwelling regions, as well as

1   a significant spatial gap within the California Current system between the Southern California

2   Bight and Oregon.

4   An improved understanding of coastal upwelling fauna is also important for interpreting the

5   paleoclimate record of these conditions (Reynolds and Thunell, 1986; Naidu and Malmgren,

6   1995; Vénec-Peyré and Caulet, 2000; Ishikawa and Oda, 2007). Many modern surveys have

7   characterized upwelling-associated foraminifera through plankton tow and sediment trap

8   studies in the tropics and sub-tropics (e.g. Thiede, 1975; Naidu, 1990; Thunell and Sautter,

9   1992; Pak et al., 2004; Salgueiro et al., 2008). Temperate and subpolar upwelling

10   communities such as those found along the Central California shelf, however, remain poorly

11   understood. On-shelf assemblages are particularly important for regions dominated by coastal

12   upwelling processes where the alternation between upwelling and relaxation (periods of

13   reduced wind-strength in between upwelling periods) has large regional impacts on

14   oceanography and planktic communities (Botsford et al., 2006; Dugdale et al., 2006; Largier

15   et al., 2006; Garcia-Reyes et al., 2014). From a paleontological perspective, modern nearshore

16   assemblages are of interest because sediments in these regions are among those most likely to

17   contain a preserved carbonate fossil record, and thus intact fossil assembalges, due to the high

18   sedimentation rates and the limitations of a narrow continental shelf above a shallow

19   lysocline.

21   Understanding planktic foraminiferal assemblages in coastal upwelling regions is also

22   relevant for predicting future climate and ecosystem perturbations. The California Current and

23   other Eastern Boundary Current upwelling systems have been identified as especially

24   susceptible to ocean acidification due to the incorporation of anthropogenic CO_2 into the

surface ocean superimposed on naturally corrosive waters (Feely et al., 2008; Hofmann et al., 2010; Hauri et al., 2013). The pronounced influence of upwelling in this region is also likely to intensify due to 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 and calcite 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 saturation state, and potentially tolerant of low calcite saturate state 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

1 associated with upwelling. These efforts may offer a general framework for interpreting

2 seasonality in foraminiferal records drawn from analogous oceanographic regions, and could

3 yield new insights into how this important group of marine calcifiers responds to ongoing

4 climate change and acidification in coastal upwelling systems.

5 **1.1 Regional Setting**

6 The California Current is the southward flowing arm of the North Pacific Subtropical Gyre

7 and along with the seasonal Davidson Countercurrent, flows adjacent to the Central

8 Californian coastline to the west of our study sites. At many locations along the coast, wind-

9 driven coastal upwelling brings deeper, colder, nutrient rich and low-O_2 water to the surface,

10 with the strongest upwelling signal found in a 10 to 25 km band just offshore (Hickey and

11 Guillery, 1979; Huyer, 1983; Lynn and Simpson, 1987).

13 At the latitudes of our study sites (37°– 39°N), wind-driven coastal upwelling is generally

14 strongest in April-June (García-Reyes and Largier, 2012). During the upwelling season, wind-

15 driven upwelling events are interspersed with relaxation periods, the combination of which is

16 responsible for large changes in productivity in the plankton (Botsford et al., 2006; Dugdale et

17 al., 2006; Largier et al., 2006; Garcia-Reyes et al., 2014). During the upwelling season,

18 further complexity is introduced through the advection of upwelled water masses both away

19 from the continent and alongshore, with water parcels in the region which are dominantly

20 sourced from the north (Kaplan and Largier, 2006). Outside of the upwelling season

21 (~September-March), upwelling events are generally absent and there is occasional

22 occurrence of downwelling, with net northward flow of water. Advection rates are variable,

23 but have been reported in the range of 10-30 km d^{-1} (Kaplan and Largier, 2006). This stable

24 post-upwelling season generally lasts into December when the stability can be punctuated by

1 storm conditions (Kaplan and Largier, 2006; García-Reyes and Largier, 2012). Together,

2 these conditions create an environment of strong seasonality in terms of productivity,

3 temperature, O_2, carbon chemistry and water mass, all of which would be expected to

4 influence the species of planktic foraminifera present in the region.

2   Methods

2.1   Study Area

7 Plankton collection took place at 8 stations located at increasing distances from shore across

8 the continental shelf (Fig. 1). Bodega Line (BL) (38°) sites start at nearshore station BL1, 1

9 km offshore, and extend across the shelf, to station BL5, 32 km offshore. These stations were

10 sampled monthly to bimonthly from September 2012 to September 2014. Three additional

11 stations were sampled in 2013 and 2014 as part of the Applied California Current Ecosystem

12 Studies (ACCESS) cruises (three times per year), and are located just over the shelf break at

13 40-60 km offshore, spanning a latitudinal range from 37°– 39°N (Table 1). All sampling

14 stations are shoreward of the central core of the California Current (Lynn & Simpson, 1987)

15 and are strongly influenced by both spring/summer upwelling as well as winter storms (Fig.

16 1).

2.2   Sample Collection

18 Vertical net tows integrated foraminifera across the water column from the surface to a depth

19 of 200 m or to 10 m above the sea floor at shallower sites. All foraminifera were sampled with

20 a 150 μm mesh net. This approach potentially excludes juveniles and small adults, and

21 therefore limited samples to foraminifera of readily identifiable adult developmental stages

22 and to species normally included in fossil analyses. Most samples were placed in ambient

23 surface seawater and kept chilled without further preservation to be picked immediately upon

24 return to shore. When this procedure was not feasible, samples were preserved shipboard in

1   95% ethanol, buffered to a pH > 8.5 with Tris(hydroxymethyl)aminomethane. Foraminifera

2   were picked wet from bulk tow material, rinsed in DI water and archived in slides. All

3   archived foraminifera were identified to the lowest possible taxonomic level, with *N.*

4   *incompta* and *N. pachyderma* defined primarily by shell coiling direction (sensu Darling et al.,

5   2006). No distinction was made between living and dead individuals although almost all

6   shells still contained some cytoplasm at the time of sorting. Taking into account the

7   conservative end of the range of sinking rates for shells (e.g., 29-552 m day^{-1}; Takahashi and

8   Be 1984) and that foraminifera were sampled from the upper 200m of the water column, we

9   can assume that all foraminifera were likely alive within 6 days of collection. Transport data

10 from the region allows us to further estimate a maximum horizontal transport of 50km in 5

11 days, indicating that all shells still within the water column were locally sourced (Kaplan &

12 Largier, 2006).

13 **2.3   Environmental Measurements**

14 Water column profiles for temperature, salinity, dissolved O_2 (DO) and fluorescence were

15 obtained across the plankton tow depths using a Seabird Electronics SBE 19 conductivity-

16 temperature-depth (CTD) profiler. Plankton tow nets were equipped with a flow meter for

17 each cast; however, due to frequent failures, flow rates were unreliable and are not reported

18 here. At each station, discrete bottle samples of surface water and water from the bottom of

19 each CTD cast were collected using a Niskin sampler. All water samples were analysed

20 spectrophotometrically for pH (total scale) using either a Sunburst SAMI (Submersible

21 Autonomous Moored Instrument) modified for benchtop use (SD +/- 0.009) or an Ocean

22 Optics Jaz Spectrophotometer EL200 (SD +/- 0.003) using *m*-cresol purple (Dickson *et al.*

23 2007). Total alkalinity was determined via automated Gran titration on a Metrohm 809

24 Titrando (SD +/- 2.809 µmol/kg), with acid concentrations standardized to Dickson certified

1 reference materials (A. Dickson, Scripps Institution of Oceanography, CA, USA).

2 Measurements of pH and alkalinity were carried out at UC Davis Bodega Marine Laboratory

3 and used to calculate other inorganic carbon system parameters, including calcite saturation

4 state (Ω_{Ca}) and [$CO_3^=$], using the software CO2Calc (Robbins et al., 2010). Thermocline

5 depths were defined as the depth (below 5m) at which the greatest gradient in temperature

6 occurred, exclusive of any temperature change with a slope of less than 0.1°C m^{-1}, in which

7 case the thermocline was assumed to be deeper than the profiled water. Upwelling index is

8 taken   from   the   PFEL   upwelling   index   modelled   for   39°N

9 (http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling.html),

10 which is in general agreement with temperature measurements from the Bodega Ocean

11 Observing Node (BL 1).

12 **2.4 Data Analysis**

13 For the four most abundant species, *G. bulloides, Turborotalia quinqueloba, N. incompta,* and

14 *N. pachyderma,* we performed a CCA (Canonical Correspondence Analysis) on relative

15 abundances using the 'vegan' package in R (R Core Team, 2013; Oksanen, J. et al., 2016).

16 Potential explanatory variables included day of the lunar cycle relative to the new moon,

17 upwelling index, duration of sustained upwelling as indicated by the PFEL upwelling index,

18 surface and deep water carbonate system parameters, and CTD temperature, salinity,

19 fluorescence, and DO. CTD data were binned into depths at 5m intervals to a depth of 25 m

20 and then at 10m intervals. A subset of variables was selected for CCA by exclusion of all

21 variables not related to any total abundances by pairwise correlation at a 95% confidence

22 level. Strongly interrelated or redundant parameters were additionally excluded (i.e. a

23 parameter correlated at multiple consecutive depths would have been considered at only one

24 of these depths).

3   Results

The assemblage was heavily dominated by the planktic species *N. pachyderma*, *N. incompta*, *T. 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*, *Globorotaloides hexagonus, Globigerinella 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 *T. quinqueloba.* A bloom of *N. pachyderma,* seen here as an increase in total abundance to > 200 individuals, occurs in July or August, after several months of sustained upwelling, followed by a decrease in both total and relative abundance to less than 50% by the end of summer (Fig 3). *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 3). In both years, the earliest *N. pachyderma* blooms appeared to initiate farther offshore, although

1 abundances within a given samples did not appear to be directly linked to specific upwelling

2 events.

4 Following the end of the summer season, the Fall-Winter fauna shows a more even

5 distribution of species and a distinct shift in the ratio of *N. pachyderma* to *N. incompta* (Fig

6 3). *N. incompta* was equally or more abundant than *N. pachyderma* during the non-upwelling

7 season although it was present year-round. *G. bulloides* also began to appear in the water

8 column in the fall, strongly associated with non-upwelled waters, and is present throughout

9 the winters. *G. bulloides* was present primarily in the winter and either absent or found only in

10 very low numbers during the summer season.

12 The same suite of species was present at nearshore stations BL1 and BL2, however, counts

13 were lower year-round and most seasonal patterns seen offshore were not evident. *N.*

14 *pachyderma* did appear to increase in relative abundance during the summer at these stations,

15 but remained in low abundance along with *N. incompta* year-round (Fig 4). *T. quinqueloba*

16 was also observed year-round at these nearshore stations. A greater proportional abundance of

17 *G. bulloides* was seen during the fall and winter at nearshore sites, consistent with findings at

18 the offshore stations (Fig 4).

19 **3.1 Environmental Measurements**

20 In spring and summer, surface hydrographic conditions were highly variable, reflecting

21 alternating upwelling events and relaxation periods. Frequent changes in thermocline depth

22 were observed, as well as intermittent blooms of near-surface productivity (Fig. 2). This

23 resulted in 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 ($\Omega_{Ca}<1$), and display low DO (<4 mg/L at <90 m) (Fig 5). 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. 5), and $\Omega_{Ca} > 1.5$ throughout the sampled water column. 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 Canonical Correspondence Analysis

A CCA shows that the highest relative abundances of both *G. bulloides* and *N. incompta* fall along dimensions strongly influenced by environmental variables characteristic of non-upwelling season, such as higher temperatures and increased dissolved oxygen. The highest relative abundances of *N. pachyderma* are most closely associated with fluorescence, especially near the surface (5m) and at 60-70 m water depth, more associated with upwelling waters. *T. quinqueloba* is also distinct, falling within the quadrant most associated with tows taken during upwelling (Fig 6). Figure 5 additionally shows the range of environmental conditions captured by sampling around the full moon (lunar days 14-18).

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 sinisterly coiling) and *N. incompta* (primarily dextral coiling) (Darling et al., 2006). 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 7).

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. *T. 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* increased in both total number and relative abundance in the late summer months following the onset of upwelling. *G. bulloides* is largely confined to the winter non-upwelling season while *N. incompta* is present in all seasons. The year-round presence of *N. incompta*

1 combined with the high summer abundance of *N. pachyderma* creates the appearance of a

2 seasonal switch in the relative abundances of the two Neogloboquadrinids (Fig 3). These

3 trends are described in more detail for each of the four species below.

4 ### 4.1.1 Neogloboquadrinids

5 The seasonal trade-off observed at offshore stations between *N. pachyderma* and *N. incompta*

6 is in agreement with previous studies interpreting seasonality from the geochemistry of the

7 two species. Sediment trap data from the Western North Pacific found that *N. incompta* and

8 *G. bulloides* reflect winter sea-surface temperature while *N. pachyderma* reflects summer

9 (Sagawa et al., 2013). Similarly, Mg/Ca ratios in recent fossils from the Norwegian Sea

10 indicate that *N. pachyderma* is primarily a summer bloom species while *N. incompta* records

11 winter conditions (Nyland et al., 2006). The close association between *G. bulloides* and *N.*

12 *incompta* seen here has also been noted previously both in the water column and in coretop

13 records (Reynolds and Thunell, 1986; Giraudeau, 1993; Ufkes et al., 1998).

15 The ratio of *N. pachyderma* to *N. incompta* (previously *N. pachyderma* var. sinistral and *N.*

16 *pachyderma* var. dextral respectively) has long been recognized to be paleoceanographically

17 significant in marine sediments, with *N. pachyderma* associated with subpolar water masses,

18 *N. incompta* associated with sub-tropical to temperate waters, and the ratio between the two

19 acting as a proxy for sea-surface temperature (Ericson, 1959; Bandy, 1960; Kennett, 1968; Bé

20 & Tolderlund, 1971; Vella, 1974; Arikawa, 1983; Reynolds & Thunell, 1986). The

21 relationship observed here between coiling direction of Neogloboquadrinids and temperature

22 is weak, at best, at the surface. The relationship is slightly stronger at 40 m depth (Fig 7), with

23 an equal ratio between *N. incompta* and *N. pachyderma* found around 10.5°C. This ratio can

24 largely be explained by the year-round presence of *N. incompta*, punctuated by an increase in

1 *N. pachyderma* in the summer along with cooler temperatures, especially in the sub-surface.

2 These findings validate on short time-scales what has been seen to be empirically true over

3 longer time-scales: *N. pachyderma* is found primarily in high latitude waters and, when

4 occurring in temperate regions, occurs mixed with *N. incompta*, whether in the water column

5 or sediment. This pattern is suggestive of an incursion of these cooler, northern waters and not

6 solely the impact of upwelled waters in this region (<10°C conditions).

7 *4.1.2 Globigerina bulloides*

8 *Globigerina bulloides* has previously been associated with active upwelling in Southern

9 California (Sautter & Thunell, 1991; Field et al., 2006) and the Arabian Sea (Peeters et al.,

10 2002). Observations along the Central California shelf are in direct contrast to this, with *G.*

11 *bulloides* observed to be far more abundant during the fall/winter relaxation and storm season

12 (Fig 3). It is notable that in at least one previous study, *G. bulloides* has shown a bimodal

13 abundance in Southern California, with one population of *G. bulloides* associated with winter,

14 and another population with the spring/summer upwelling season (Sutter & Thunell, 1991).

15 Furthermore, two distinct genotypes of *G. bulloides* have been identified in Southern

16 California, one of which is present in winter samples and was previously recognized in

17 "subpolar" regions (Darling et al., 2003). We interpret the *G. bulloides* observed along the

18 Central California Coast as connected to this "subpolar"/winter population, accounting for the

19 differences in seasonal abundance seen at our Northern site compared to Southern California.

20 *4.1.3 Spatial Dynamics*

21 Nearshore stations BL1 and BL2 are shoreward from the primary band of coastal upwelling

22 (Huyer, 1983) and show less seasonality in species abundances with the exception of *G.*

23 *bulloides,* which is more abundant in the fall and winter nearshore as well as offshore.

24 Although non-spinose forms are also occasionally present at both nearshore sites, they do not

1   show the seasonality that they do at offshore sites (Fig 4). Some of the differences seen in the

2   fauna at BL1 and BL2 compared to offshore stations may be due to shallower tow depths at

3   these sites (25 m and 45 m, respectively), and therefore a bias in favor of species living closer

4   to the surface, which may include *G. bulloides*. However, shallow tows conducted at BL4 and

5   BL5 confirm that all four species considered here are present in the upper water column (<30

6   m) at these sites, so depth alone cannot completely account for the nearshore/offshore

7   difference in foraminiferal abundances. Nearshore stations may be sheltered from larger-scale

8   transitions in source water that happen over most of the shelf, and more impacted by

9   terrestrial processes.

11   Short-term spatial dynamics were also observed to impact foraminiferal abundance. On days

12   when overall productivity was low, abundances of all foraminifera species was higher at sites

13   with higher fluorescence (indicating higher biomass and suggesting higher primary

14   productivity). Especially low fluorescence (near-surface fluorescence <2) was observed on

15   collection days 2/4/2013, 1/16/2014, 7/1/2014 and 2/26/2013. On these days, foraminifera

16   were recovered in much greater numbers at stations associated with peak fluorescence

17   regardless of where along the transect the station was located (Fig 8). On 1/16/2014 no

18   foraminifera were recovered at very low productivity stations BL1, BL5 or on 7/1/2014 at

19   BL1, while other sites yielded >100 individuals. On 2/4/2013, BL2 was associated with the

20   only observation of surface fluorescence >10 and yielded more foraminifera than all other

21   sites combined. Fluorescence was low at all sites on 2/26/2013 and no foraminifera were

22   recovered from these tows (Fig 8). These data indicate that phytoplankton productivity may

23   ultimately be a limiting factor for all species. On days with higher measured fluorescence

1 (productivity), the dominant spatial trend was towards higher abundances further offshore

2 regardless of where peak productivity was observed.

4.1.4 Foraminifera in Reduced pH Waters

4 Upwelling associated waters with low Ω_{Ca} were observed on multiple occasions during

5 plankton tows. Foraminifera are widely thought to be susceptible to ocean acidification (i.e.

6 Barker and Elderfield, 2002; Manno et al., 2012; Moy et al., 2009; Orr et al., 2005), although

7 this susceptibility may not always manifest through a reduction in shell weight in open ocean

8 conditions (i.e. Beer et al., 2010; Aldridge et al., 2012; Weinkauf et al., 2016). The

9 association of multiple species of foraminifera already living at $\Omega_{Ca} < 1$ or very low Ω_{Ca} (<1.5)

10 waters is notable. In particular, more than a quarter (26%) of all observed *N. pachyderma*,

11 with its strong upwelling association, were found to occur in a water column with $\Omega_{Ca} < 1$ in

12 the upper 160m. Culture studies with this species have indicated a decrease in shell weight

13 associated with low Ω_{Ca} well within the range of those that *N. pachyderma* was found in

14 during upwelling season, indicating the potential to impact carbonate flux in areas where this

15 organism is an important calcifier (Manno et al., 2012). If *N. pachyderma* is already living

16 near its Ω_{Ca} tolerance, this species may be exceptionally vulnerable to a continued increase in

17 ocean acidification in this region. However, it is possible that upwelling-adapted *N.*

18 *pachyderma* may prove to be an example of acalcifying plankton able to tolerate

19 undersaturated waters.

4.2   Causes of Seasonality and Fluctuations in Abundance

21 Seasonality has previously been identified in temperate regions globally for all four of the

22 species addressed here (Jonkers & Kucera, 2015). One important mechanism contributing to

23 the seasonal progression of foraminifera species along the shelf in Central California is the

24 alternation between the direction of net water transport between upwelling and non-upwelling

1   seasons. This phenomenon would account for the occurrence of *G. bulloides* in greater

2   numbers outside of upwelling season when net poleward water transport is expected (Kaplan

3   and Largier, 2006). Similarly, the influx of subpolar associated *N. pachyderma* could be due

4   to this species being carried into the region during the southward transport of water that

5   occurs during upwelling season (Kaplan and Largier, 2006). This is in slight contrast to the

6   hypothesis of *N. pachyderma* dormancy outside of upwelling season suggested in the Arabian

7   Sea (Ivanova et al., 1999), since in the California Current as well as on the Namibian margin

8   there is some synchronicity between the preferred seasonality of *N. pachyderma* and greater

9   transport into the region from high latitude waters (Fumes & Zachariasse, 1993). An

10   alternation between the foraminiferal fauna of source waters additionally offers an

11   explanation for the seasonal absence and reappearance of both *N. pachyderma* and *G.*

12   *bulloides*. *N. incompta,* found year-round in the study region, may be present in both water

13   masses.

15   In addition to the broad oscillation of source waters, higher counts of each species are

16   associated with some specific water column characteristics. In most cases, species abundances

17   could not be linked strongly to single environmental parameters, but rather a suite of

18   hydrographic and temporal variables were required to account for faunal assemblages. For

19   some species, particular variables can be identified through pairwise correlation as having a

20   significant effect on abundance (Fig. S2). In *G. bulloides*, higher abundance correlates with

21   higher water temperatures throughout the water column. In *N. pachyderma*, higher

22   abundances are associated with higher fluorescence, and thus enhanced primary production.

23   For *N. incompta,* counts seem to loosely correlate with higher O_2 and lower salinities, while *T.*

24   *quinqueloba* is not clearly correlated with any single measured parameter (Fig S2).

2 A CCA shows the relative abundances of *G. bulloides, N. incompta* and *N. pachyderma* to be

3 dependent upon environmental variables strongly associated with coastal upwelling

4 conditions (Fig 6). However, the directions of those associations vary. *N. pachyderma,* and to

5 a lesser extent, *T. quinqueloba,* seem to be associated with upwelling-like water conditions.

6 Sediment trap time series have previously linked *T. quinqueloba* to productivity in the North

7 Atlantic (Chapman, 2010), which could explain the association of this species with the higher

8 productivity season, although it is not directly associated with shifts in productivity as is *N.*

9 *pachyderma. G. bulloides*, however, is negatively associated with upwelling-like water

10 conditions, and more associated with warmer waters and higher DO levels seen outside of

11 upwelling season. *N. incompta* relative abundances also increase outside of upwelling season,

12 although in this case, relativity may be key, especially with regards to *N. pachyderma* (see

13 4.1.1). This outcome is supported by total counts, which indicate that this species is the only

14 one clearly present at the tow sites year-round.

15 *4.2.1 Lunar Periodicity*

16 Abundances of *G. bulloides, T. quinqueloba, N. incompta* and *N. pachyderma* all display an

17 abundance cycle with a 28-day period that appears to coincide with the lunar cycle (Fig. 9).

18 Peak counts for each species occur within 7 days of the full moon, before dropping off before

19 the new moon (Fig 8). This trend offers further evidence that planktic foraminifera reproduce

20 on a lunar cycle (Spindler et al., 1979; Bijma et al., 1990; Bijma et al., 1994; Schiebel et al.,

21 1997; Jonkers et al., 2014; Venancio et al., 2016). The peak abundance for *G. bulloides* occurs

22 before that in the other species, starting 3 days before the full moon and remaining high until

23 4 days after the full moon. Abundances in *N. pachyderma* and *N. incompta* begin to increase

24 around the same time, but high abundances in these species continue until 5 and 7 days after

1 the full moon respectively. Whether the observed offsets in peak abundance around the full

2 moon represent inter-species differences in reproductive timing or are an artefact of sampling

3 against a background of strong seasonality in a highly variable environment cannot be

4 resolved from this dataset, even though sampling days surrounding the full moon occurred

5 across seasons (Fig 5).

6 ## 4.3 Application to the Fossil Record

7 The presence of seasonally distinct faunas along the Central California margin can be used in

8 increasing the resolution of paleoceanographic and paleoecologic records, as different species

9 clearly represent different states of the seasonal upwelling regime. Single-species

10 geochemical records are likely to show a strong bias towards either upwelled or non-upwelled

11 water masses, and therefore, could potentially be harnessed as a record of changes in

12 upwelling intensity and associated water chemistry. Our findings reaffirm a strong

13 relationship between the dominance of *N. pachyderma* in conditions favourable to upwelling.

14 This pattern has been noted along the African margin (Giraudeau, 1993), in the Arabian Sea

15 (Ivanova et al., 1999), and on the Namibian margin (Ufkes & Zachariasse, 1993). It remains

16 possible that other genotypes of *N. pachyderma* have distinct and ecological preferences

17 particularly those associated with the Arctic and Antarctic (Darling et al., 2006; Darling et al.,

18 2007). As our record is based on discrete tows and not a continuous record, the percent

19 composition of species cannot be directly translated into a sediment flux or to what would be

20 preserved in aggregate in the fossil record. However, the upwelling season bloom of *N.*

21 *pachyderma* seen here is strong enough that this signal would likely dominate the annual

22 assemblages, although the vast majority of *N. pachyderma* (81% of those seen in tows) occur

23 between July and November.

1   *Globigerina bulloides* has been associated with upwelling at other sites globally (Sautter &

2   Thunell, 1991; Peeters et al., 2002; Field et al., 2006) and even used as an upwelling indicator

3   in the fossil record (e.g. Naidu, 1990; Kroon et al., 1991; Anderson & Prell, 1993; Naidu &

4   Malmgren, 1996). However, within our study region, this species was present almost

5   exclusively outside of upwelling season. The majority (88%) of the *G. bulloides* seen in our

6   samples was observed between November and February. CCA supports these observations in

7   indicating that the relative abundance of this species is negatively associated with upwelling-

8   like conditions in the region. This situation contrasts with findings in Southern California and

9   the Oman Margin (Peeters et al., 2002; Field et al., 2006), highlighting the importance of

10   using regionally specific associations where possible when interpreting planktic assemblages

11   in the sediment record.

13   **5   Conclusions**

14   Surveys of planktic foraminifera retrieved from plankton tows both confirm and contrast with

15   findings of studies in analogous regions. Along the North-Central California shelf there is a

16   clear association between upwelling and *N. pachyderma,* which experiences a summer bloom

17   and increases in relative abundance, as seen at other sites. This summer population of *N.*

18   *pachyderma* appears to routinely experience low Ω_{Ca} waters, conditions that are predicted to

19   increase in the near future. *N. pachyderma* associations with upwelling and low temperatures

20   are also reflected in the empirical relationship between *Neogloboquadrinid* coiling direction,

21   seen previously in the sediment record, with a switch in dominance between *N. incompta* and

22   *N. pachyderma* at 10.5°. *G. bulloides*, however, is associated in our study with non-upwelled

23   waters, in contrast with populations in Southern California and other upwelling regions. All

24   species showed a lunar periodicity in their abundances, evidence of lunar timed reproduction.

1   This study highlights the wealth of information on seasonal-scale processes that is contained

2   within foraminiferal shells. To access this information, however, it is of great importance to

3   ground interpretations of foraminiferal proxies in species and regional ecology to the greatest

4   extent possible.

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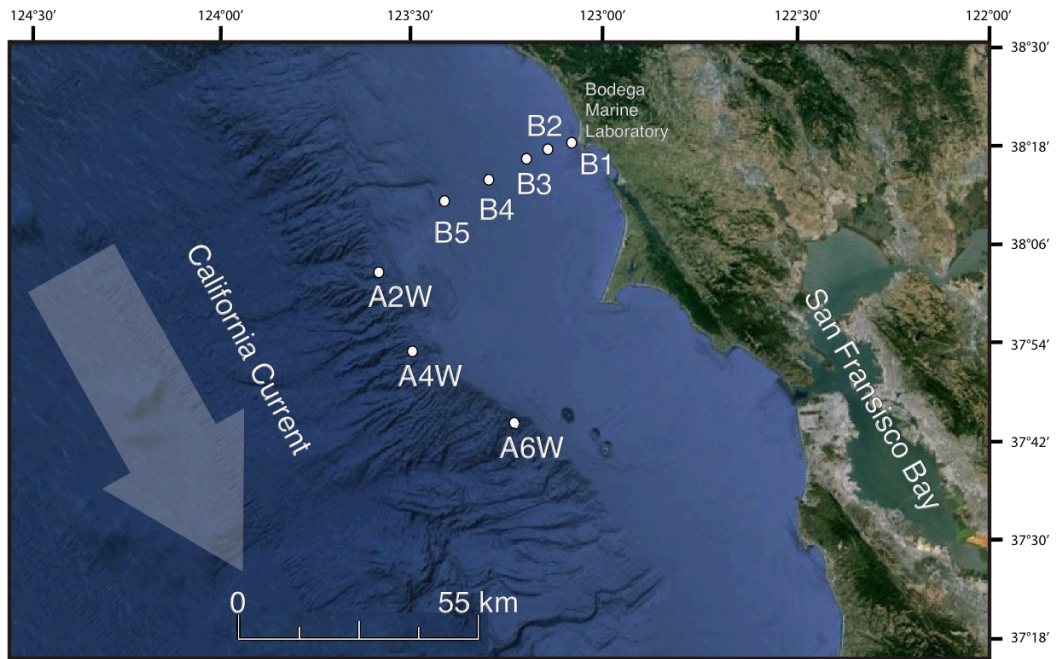
Station	Latitude	Longitude	Depth Sampled (m)	# Times Sampled
BL1	38° 16' 59"	-123° 04' 60"	25	15
BL2	38° 23' 38"	-123° 13' 00"	45	15
BL3	38° 21' 05"	-123° 14' 20"	90	15
BL4	38° 26' 20"	-123° 27' 01"	120	15
BL5	38° 21' 05"	-123° 37' 59"	200	14
A2W	38° 02' 45"	-123° 33' 47"	200	5
A4W	37° 52' 55"	-123°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

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

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

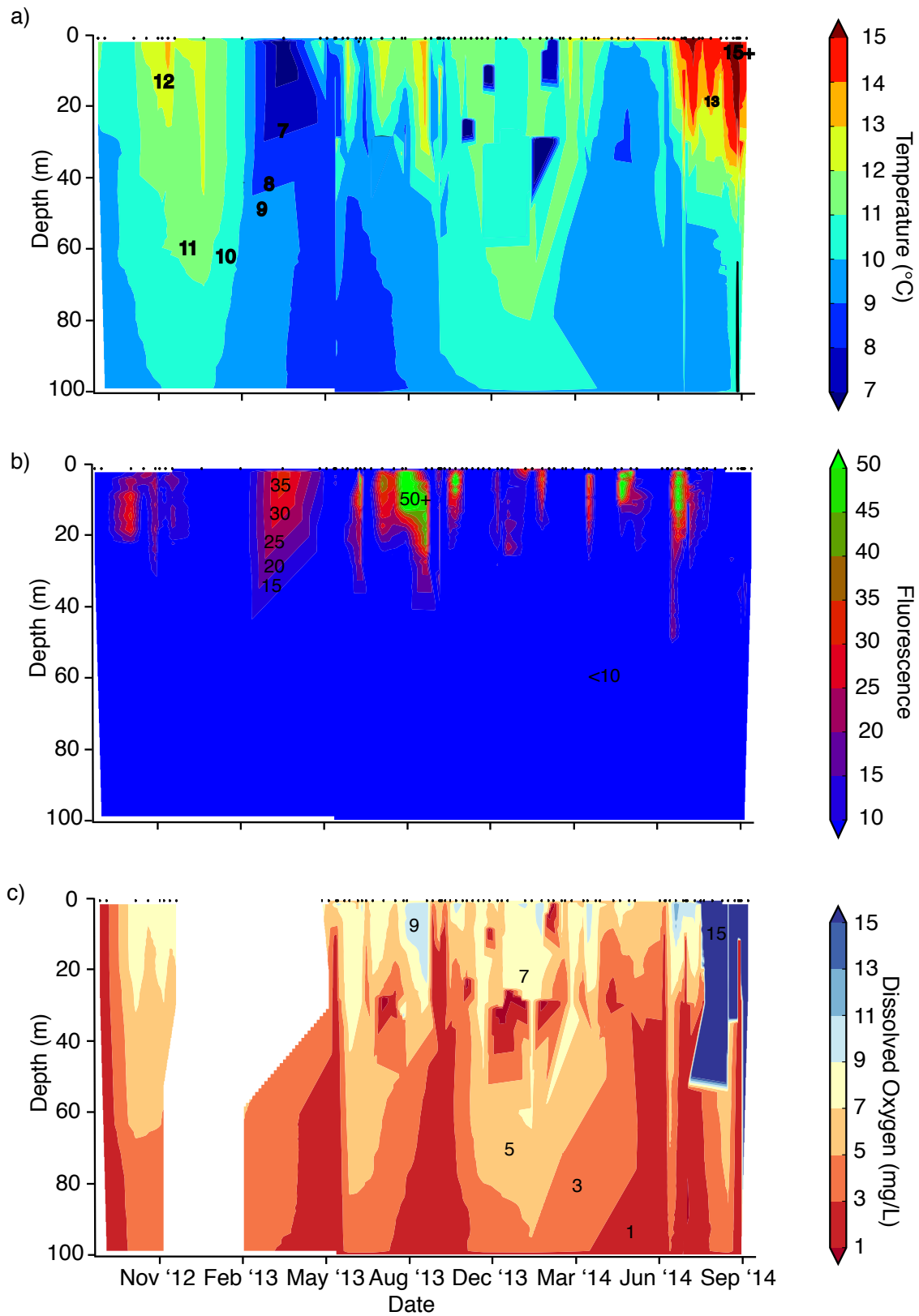
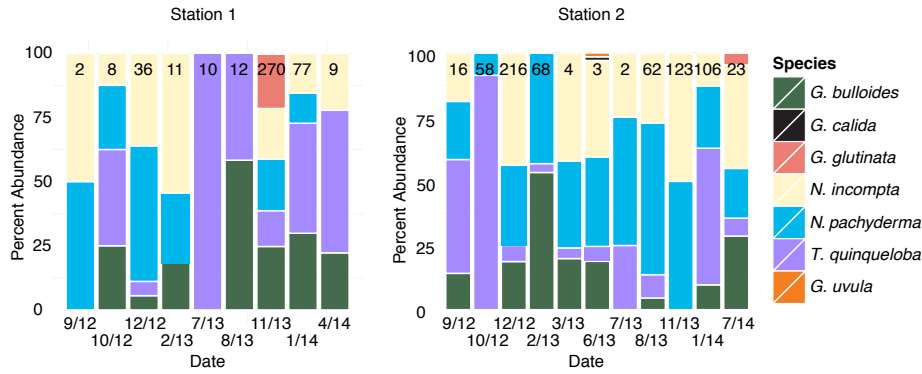
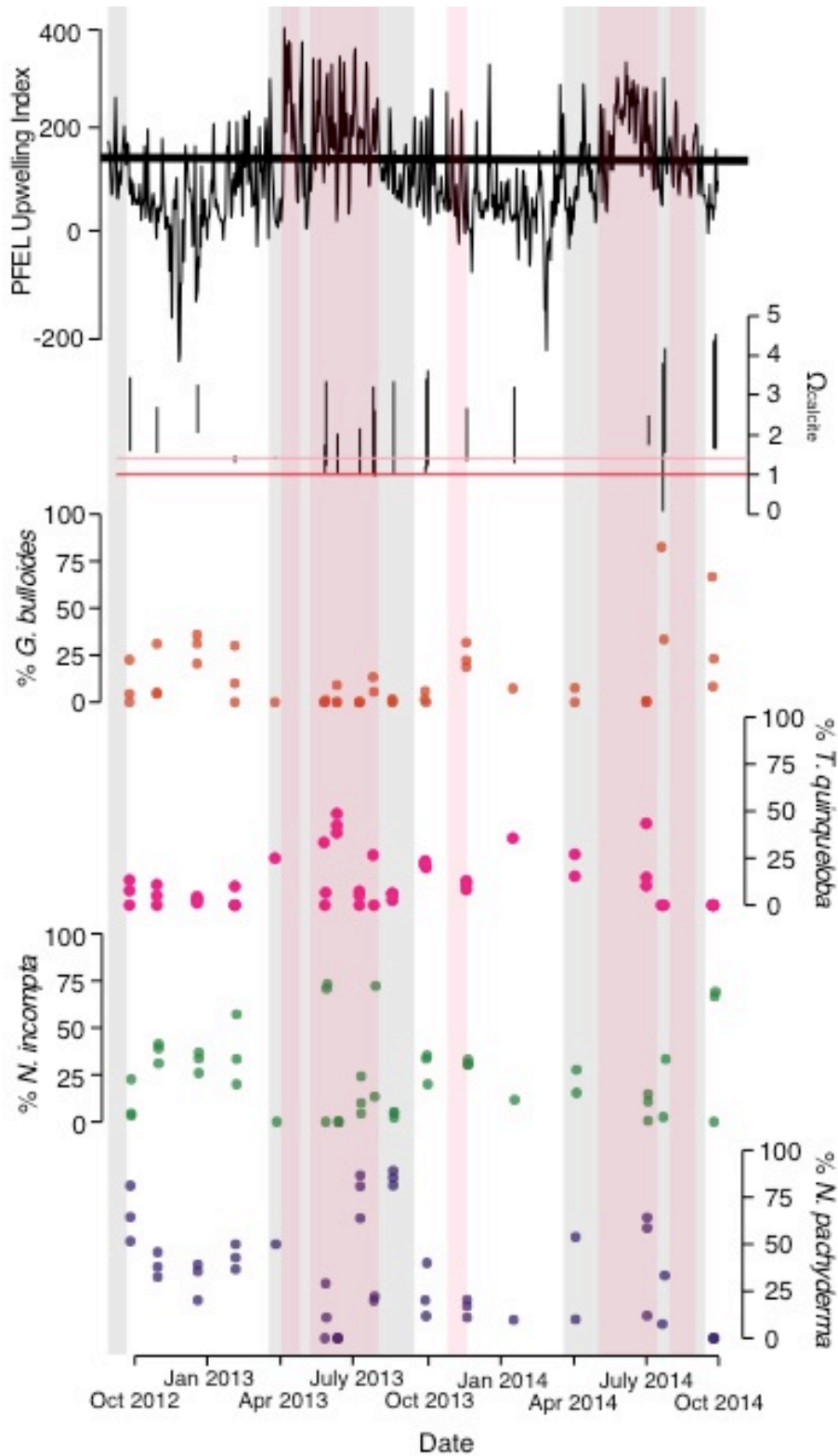



Figure 2. A time-series of CTD cast profiles for a) temperature, b) productivity, and c) DO taken between September 2012 and October 2014. Time-series are compiled from CTD casts

1   at BL5 in conjunction with plankton tows and supplemented with data from weekly CTD

2   casts taken at BL1 as a part of the Bodega Ocean Observing Node. Black points at the top of

3   each figure denote the location of each CTD cast.

6   Figure 3. Relative abundance of all species at near shore stations BL1 and BL2, with total

7   number of foraminifera marked at the top of each bar.

3 Figure 4. Upwelling index for 39°N (PFEL;

4 http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling.html),), with

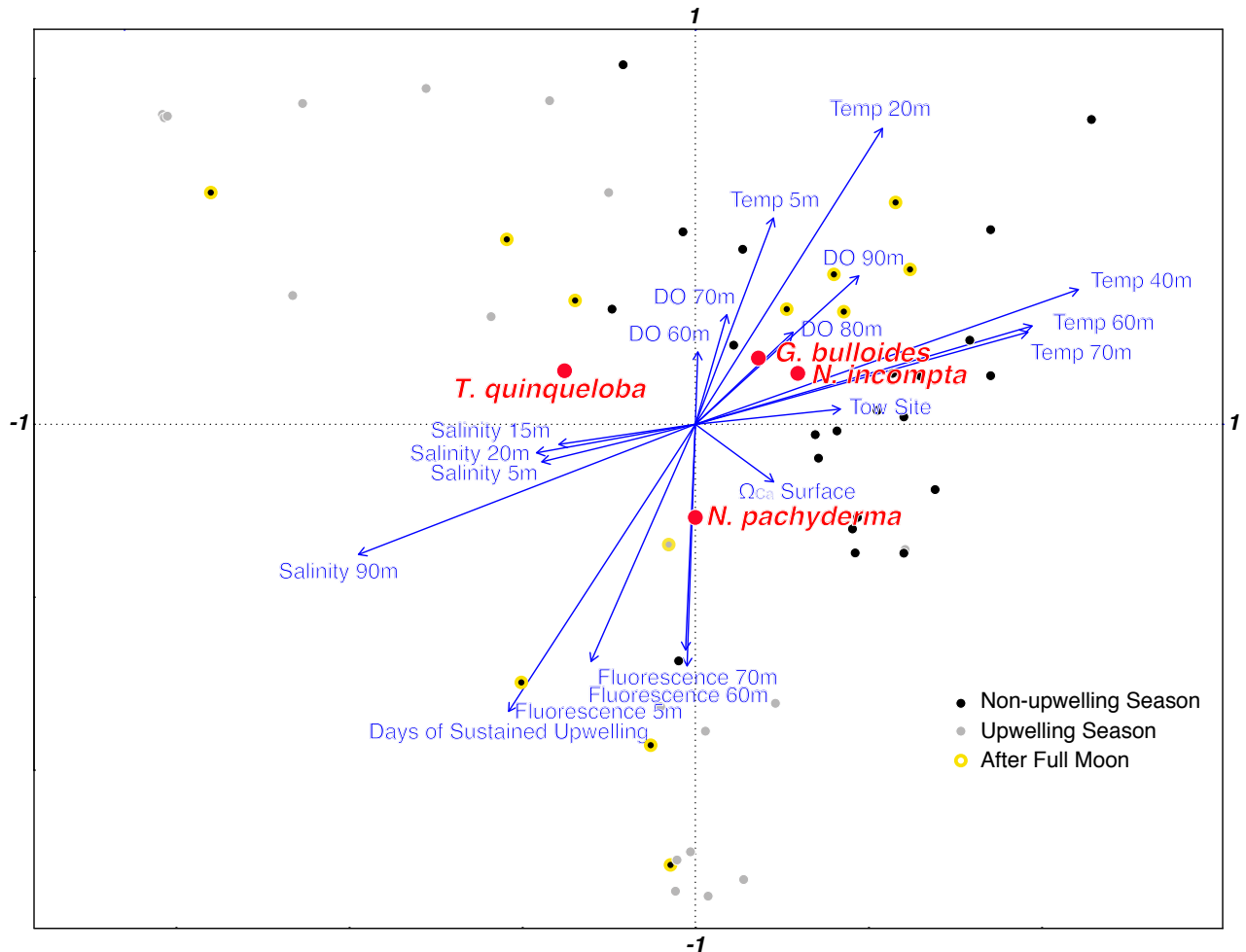
1 "upwelling season" shaded in grey, and periods of sustained upwelling conditions during the

2 relevant years shaded in red. The range of C_{alcite} observed on each tow is marked in black,

3 with $\Omega_{calcite} = 1$ marked in red and $\Omega_{calcite} = 1.5$ in pink. Percent abundances from vertical tows

4 of *G. bulloides, T. quinqueloba*, *N. incompta,* and *N. pachyderma* from offshore stations BL3,

5 BL4, BL5 and off-shelf stations AW2, AW4, and AW6 shown in orange, pink, green and

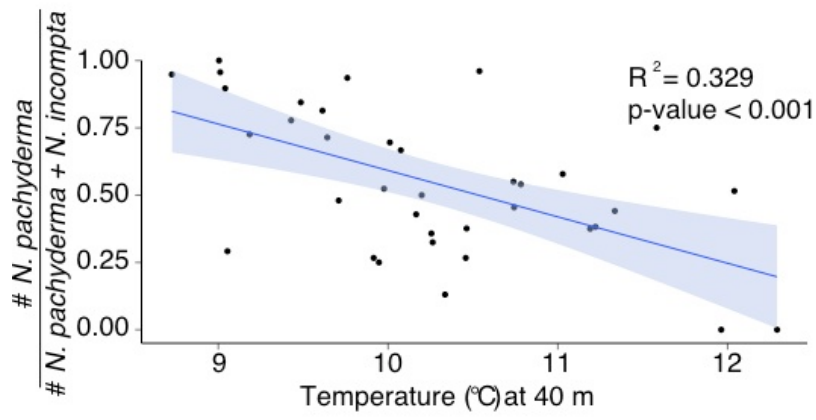
6 purple, respectively.

9   Figure 5. Biplot of Canonical Correspondence Analysis of relative abundance of the four

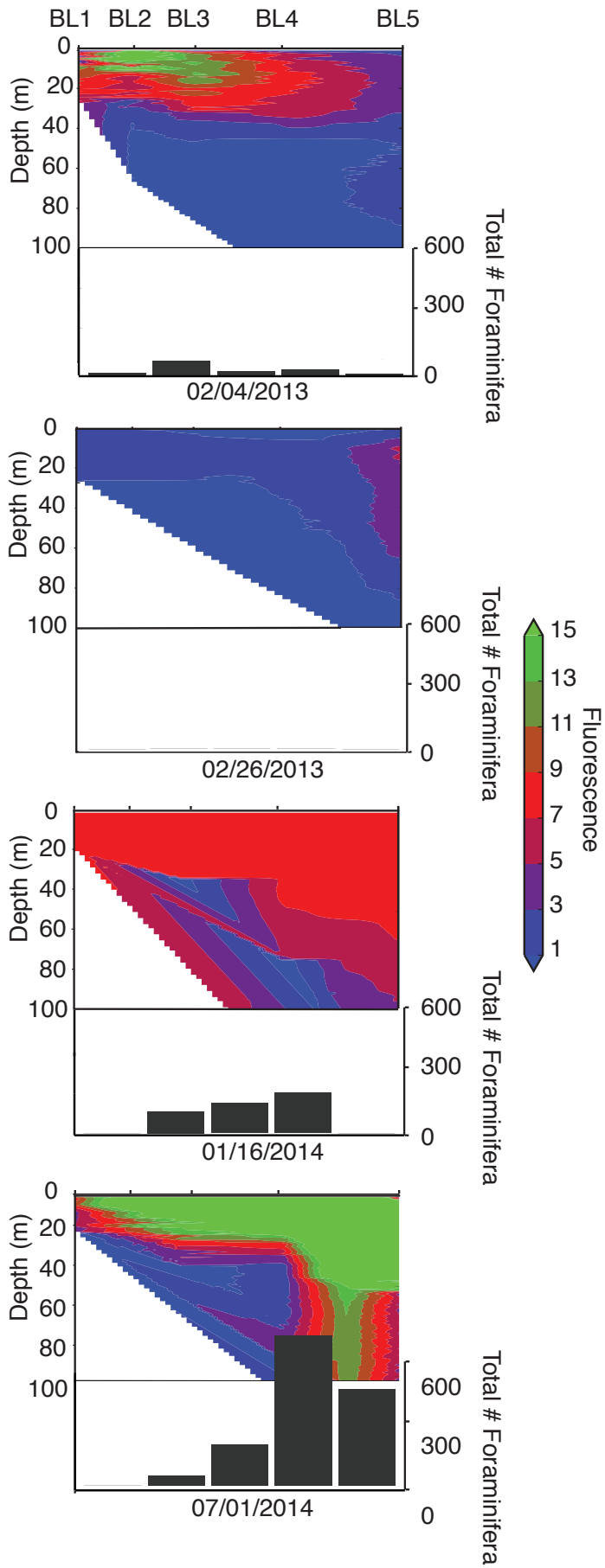
10 most abundant species compared with environmental variables at the time of collection for all

11 tows in which foraminifera were found. Dominant species are represented by large red points,

12 and small points represent individual tows. Grey points are tows that fall within upwelling

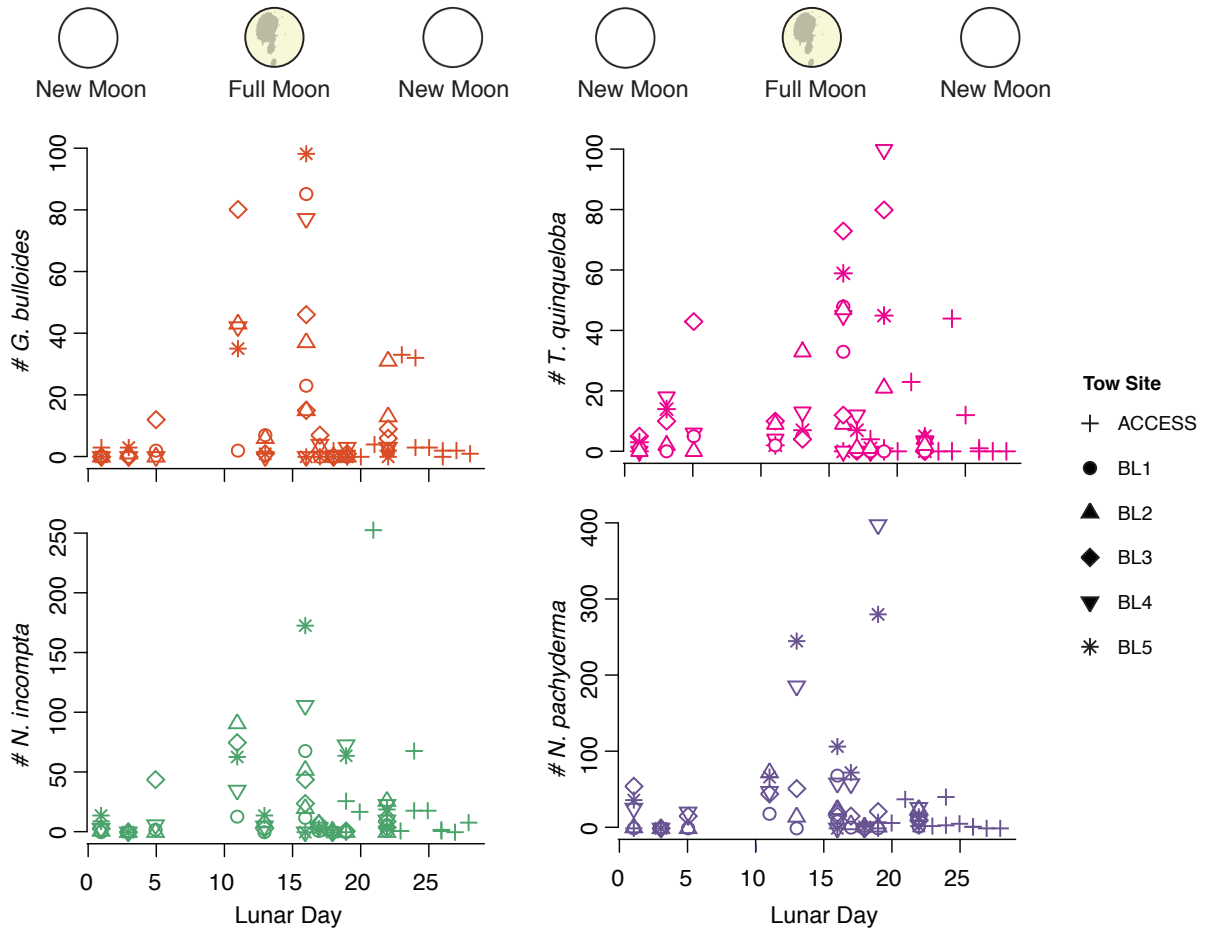
13 season, as shown in Fig. 2, and black points outside of this season. Points with a golden halo

14 represent tows during lunar days 14-18.

11   Figure 6. Ratio of *N. pachyderma* to *N. pachyderma* and *N. incompta* at 40m depth with 95%

12 confidence envelopes.

1   Figure 7. Water column fluorescence data and total number of foraminifera recovered at

2   stations BL 1-5 on four days of extremely low productivity. CTD data from these 5 stations

3   demonstrates small-scale variability from 1 to 32 km offshore along the continental shelf, and

4   compared this with the total number of foraminifera retrieved at each of these stations.

8   Figure 8. *G. bulloides, T. quinqueloba*, *N. incompta,* and *N. pachyderma* counts by lunar day

9   from the new moon (Day 0) to Full Moon (Day ~14). Abundances are taken from integrated

10   tows, at 25 m, 45 m, 90 m, 120 m and 200 m depending on the station (see Table 1). Symbols

11   denote tow station.