Response to Reviewer Comments:

We would like to thank the three anonymous reviewers for their comments and suggestions. Our manuscript will be greatly improved by incorporating these changes, and we are grateful for the time and care taken in reviewing this manuscript. Below we discuss major/significant changes and address specific suggestions.

1) Clarification of methodology: All three reviewers highlight a limitation of our dataset, in that due to frequent failure of our flow meter, we cannot be confident in interpretations of our data as a volumetric abundance (foraminifer/m^3). We have attempted to not over-interpret this portion of our dataset. This was mentioned briefly in our methods section, but as it is clearly an important point, will be expanded upon in section 2.2 of a revised manuscript, and we will endeavor to make this aspect of our methodology more clear throughout.

2) Greater emphasis on relative abundance data: In response to the specific comments of Reviewer #3, we will replace our Principle Components Analysis (PCA) with a Canonical Correspondence Analysis (CCA) utilizing relative abundances instead of log transformed total abundances. We are particularly grateful to Reviewer #3 for suggestions that led us to this revision in statistical approach. We will also move results of pairwise correlations to supplementary material. Thus, while we would include total foraminiferal abundances in a revised Fig. 2 (and a supplemental figure as suggested by Reviewer #1), we feel that presenting such data alongside relative abundance data in Fig. 4 could be misleading. We argue, however, that the presentation of total abundance data is informative enough when conservatively interpreted to be retained in the body of the paper in our discussion of lunar cycles as well as presence/absence of foraminifera in relation to localized productivity. In the later case, this may actually be a particularly informative approach as "standing stock" when comparing between sites of such different depths might introduce additional bias (i.e. we might expect a higher volumetric standing stock at a 30 m depth site than 200 m, if the dominant foraminifera population at the time have a shallower preferred depth habitat).

3) Comparison between data treatments: While we have further shifted the emphasis of our interpretations towards analysis dealing with relative abundance data, we put forward that large-scale seasonal differences in total abundance are still both interpretable and informative where other metrics are unavailable. As all tows were vertical and consistent in depth at each station and speed across all stations, one could make the assumption that the volume filtered is roughly correlated with tow depth – or really "line out," and calculate standing stock. There are currently unquantifiable errors associated with this approach, i.e. "vertical" tows are often not perfectly vertical, and current strength and high productivity "net clogging," are not accounted for. Thus while we have chosen not to include this treatment of data in the body of our manuscript, the major conclusions are not altered by use of this data treatment compared to total abundance. We would be happy to provide a figure comparing the two in the supplemental material of a revised manuscript if the editor deems it appropriate.

Point by Point Responces:

Are the counts shown on figure 8 from the integrated 200m tows?

No, these are total counts for this station, so from 25, 45, 90, 120 and 200 m depth as shown in Table 1. This is clarified in the figure caption.

Why are the environmental parameters shown only for the top 100 m?

The decision to plot only the upper 100m was due to the fact that hydrography is far less variable below 100 m, and extended plots were uninformative. Full plots to 200m are included as Supplementary material for the interested reader.

Considering that during the full moon phase the total number of a particular species of planktonic foraminifera can increase by 4-5x or even 1 order of magnitude, it would be good to have a graphic showing total abundances for each species together with the most important environmental parameters in one graphic where the different moon phases are also indicated.

All statistical approaches suggest that single environmental variables are difficult to correlate with species abundances, with the possible exception of *N. pachyderma* and high fluorescence. However, due to the limitations of our total abundance data, we would not be confident in further interpreting total abundance data in this way.

Technical Corrections: Section 3 is Results and not Methods"

Thank you to the reviewer for noticing this. It has been amended.

Show correlation matrix rather than Table 2:

A correlation matrix (replacing Table 2) is included in the Supplement to the manuscript.

Figures 2 and 7 The program used generates some very strange patterns that need to be revised.

In this case, it appears that the embedding of images may in part be responsible for poor graphic quality. All figures have been very carefully edited for clarity and ease of viewing.

Figure 3 – the graphics have to be bigger and the figure should also include the total abundance of foraminifera observed at each sampling time and station.

Revised graphics are embedded here and full-sized, high-resolution will be submitted as that option is made available. On the second part of this comment, however, we respectfully disagree with this reviewer. Due to the necessary caveats of the presented total abundances, which the reviewer also acknowledges, we would prefer to keep the two data types separate so as not to mislead the reader.

The graphs presented in the supplement file do not add any useful information other than showing that the two variables are not at all related between them in the great majority of the cases.

This supplemental figure has been removed. Especially with the inclusion of a correlation matrix for the most relevant pairs, as suggested by this reviewer, we agree that this figure is not informative.

Figure 7, which does not show the breakdown by station, and thus could also be interpreted as a migration of the upwelling core during the lunar cycle.

Fig. 7 has been ammended to code each point by station. The trend towards greater abundance of shells, however is found at all stations (as will be clarified by a revised figure as suggested) as well as regardless of upwelling seasonality.

The manuscript has a side focus on acidification, yet the carbonate system data are not shown anywhere in the figures nor in tables. Adding a panel on Figure 4 would be helpful to get a sense of the gradient.

We have added a panel to Fig. 4, demonstrating the range of $\Omega_{calcite}$ values observed during collection, along with an indication of $\Omega_{calcite} = 1$ and $\Omega_{calcite} = 1.5$.

Moreover, the idea that acidification/lower omega is systematically associated to lower calcification/shell weight has been shown not to be the case for G. bulloides in the Arabian Sea [Beer, C.J., Schiebel, R., Wilson, P.A., 2010. Testing planktic foraminiferal shell weight as a surface water [CO32-] proxy using plankton net samples. Geol 38, 103–106. doi:10.1130/G30150.1.], and thus, even if the manuscript deals on the resilience to acidification rather than the direct effect of acidification on calcification, it might be interesting to have both perspectives in the final paper.

The reviewer brings up a good point, as an increasing body of work is demonstrating a less direct link between $[CO_3^{2-}]$ and shell weight than has been demonstrated in laboratory culture. We have amended our discussion to directly address this on Page 16, Lines 6-8. It is additionally important to note that we do not assume shell thickness to be synonymous with resilience to ocean acidification, with the mechanics of both in foraminifera requiring further investigation.

The manuscript would benefit of the addition of a short paragraph describing the taxonomic rules used to differentiate N. incompta from N. dutertrei and N. pachyderma. Are the authors using N. incompta as N. pachyderma right coiling (sensu Darling et al. 2006) or are they using the former rule of intermediate forms between N. dutertrei and C2 BGD Interactive comment Printer-friendly version Discussion paper pachyderma (N. eggeri)?

We use *N. incompta* as defined by Darling et al., 2006, formerly *N. pachyderma* (dextral coiling). This is clarified on Page 12, Line 6. While we acknowledge the presence of some aberrant coiling foraminifera reported in each population, no clearly aberrant foraminifera were observed, and the possibility of such <3% as estimated by Darling et al., 2006, is unlikely to strongly effect our results.

The statistical analysis needs to be further documented : the matrix output of the PCA analysis (eigenvalues) would be very helpful. Which software was used ?

All statistical analyses were carried out using the open source R software, which will be added to our Methods section 2.4. Following suggestions by reviewer #3, the PCA will be replaced with a CCA taking into account only relative abundances (carried out using the 'vegan' package in R), now documented on Page 8, Line 14-15.

I also have some difficulties to understand the rationale for the two step PCA analysis as it just gives more variance to the selected set of species.

This analytical approach has been replaced by CCA (Fig 7; Section 3.2.

I wonder what is the impact of the very few stations with high abundances : on the supplementary plate, most of the trends, seem to be forced by a very limited set of nets : eg for incompta, removing the samples with an abundance higher that 100 would likely collapse all the trends derived.

The trends shown in the supplemental figure are indeed driven by a subset of samples, however we would argue that these are not the higher abundance samples but those that are > 0, as samples with no instances of a given species were retained for this analysis. This figure has been removed.

Minor comments : Raw data should be deposited on a permanent data repository or added in supplementary material as a table.

All of the foraminiferal abundance data will be included as a supplement. Oceanographic data are available on request from BOON (Bodega Marine Laboratory) and Point Blue (http://www.pointblue.org/datasharing). This has been added to our acknowledgements on Page 21 Line 21.

p2 l.20 : add the approximate location of station Papa

This has be included on Page 2, Line 20.

p3 l. 20 what is special in the California upwelling that it makes it "unusual"-ly sensitive to acidification. My sense is that is the most studied upwelling, but I cannot see any reason why it would be different in other upwelling regions.

This statement was not meant to suggest that the California Current upwelling system was unusually susceptible in comparison to other Eastern Boundary Current upwelling systems – and we agree with the reviewer that all are likely susceptible, although the preponderance of data refers to our system in California. Rather, this and likely other EBC upwelling systems are vulnerable compared to open ocean environments. This sentence has been rephrased to clarify on Page 3, Line 22-24.

p6. l22 : what does TRIS stand for ?

Tris(hydroxymethyl)aminomethane, added to Page 7, Line 1.

p11 l. 9-10 : to be consistent with the hydrographic description during upwelling season, please give the omega value.

p12 l. 9 : correct sinistral

p.14 l. 10 : change Globigerinoides by Globigerina

Figure 1 : please change the labels of the stations of the map to BL as in text or figure caption.

All of the above have been amended.

Figure 2 it would be helpful to add the timing of the different tows on this figure with two different sets of ids for BL and ACCESS stations.

We appreciate this suggestion, however, our best attempts to render the figure as suggested decrease clarity overall, especially as no discernable differences were found between this and BL Stations 3-5. The station breakdown will, however, be included in our tow data.

Figure 3, right panel : correct quinqueloba

This has been corrected.

Supplemental figure : please add in X-axis the unit (# of forams ?) ;

In response to comments from Reviewer #1 as well as the issues raised here about over interpretation of raw abundance data, this figure will be removed altogether.

add a caption What is the unit for fluorescence in the supplementary plate ? - note that usually a calibration can transfer the fluo signal in chlorophyll concentration, as fluo measurements are highly dependent of the sensor used (and its maintenance).

This supplementary figure has been removed from the MS at the recommendation of Reviewer #1. However, we will still address this comment as fluorescence also appears in our Fig. 2. Fluorescence is dimensionless and a link to the manufacturers webpage will be included in out Methods section. While we recognize that a chlorophyll calibration can be run, we were not able to do so over the course of this study. The same sensor was, however used for all measurements presented in Fig. 2 and consistently maintained. Thus, like all fluorescence measurements, this should be taken as a relative measurement, internally consistent for this study.

The authors must realize that a "bloom" of a species, whose abundance is expressed as percentage of the total assemblage could in fact reflect the period of the lowest standing stock of that species (as long as the standing stock of the other species is reduced even more).

This is an important point. Our assessment that *N. pachyderma* appeared in "blooms" was based on total abundance data, now states on Page 9, Line 17-18. Although we are reluctant to over interpret total abundance data, in this case the *N. pachyderma* "blooms" refer to an order of magnitude increase in the number of individuals.

Second, the multivariate data analysis if in my opinion based on inappropriate methods. It seems to be based on counts (log-transformed), which is fine, but surely these have to be normalized to volume or else they are not really informative?

Part of the rationale for using a log transformed data set was to try to interpret only the most robust trends in our count data. In response to the comments of this reviewer, we revised our approach to multivariate analyses, utilizing a CCA and relative abundance data as opposed to PCA. This removes many of the underlying uncertainties in this analysis, including use of a non-linear variable (lunar day), and confusion surrounding resulting biplots.

I believe the authors should either ask how one can explain the assemblage composition by a combination of environmental variables or they may ask how to explain the standing stock of one particular species by environmental variables. The former would require a constrained ordination, the latter a generalized linear model. Both analyses permit post-hoc parameter selection and the GLM also allows testing for interactive effects.

We appreciate the reviewer's thoughtful comments on this front and have refocused our multivariate analysis approach by utilizing a CCA approach as explanatory of assemblage composition. Due to limitations in volumetric sampling and the high degree of interaction between our variables, a GLM is probably a less ideal approach for this dataset.

Third, the detection of lunar periodicity as described in 4.2.1 is in my opinion flawed. These data cannot provide any support for the presence of lunar periodicity, because they are not derived from successive days within one lunation (and are not scaled. . .). Instead, they reflect the fact that one or two of the many sampling campaigns yielded unusually high numbers of a given species. These high values produce an impression of a peak, which happens to occur around full moon. To substantiate a claim for the existence of lunar cycle, the authors would have to prove that the sampling situation with unusually high standing stock does not represent a situation with unique hydrography, driving the standing stock high irrespective of lunar phase. This would be hard, because the authors have shown in their prior analyses that the standing stack of the analyzed species can be explained well by a combination of environmental parameters. So the high standing stock samples must reflect a unique oceanographic situation.

We agree that our data alone do not conclusively shown reproduction associated with lunar cyclicity. However, our observations are consistent with a growing body of literature demonstrating a similar trend by a variety of methods. Our findings of higher foraminiferal abundance associated with the days following the full moon hold true when scaled roughly to target net depth. We will additionally added demarcations to our CCA plot for samples which followed the new moon (Days 14-18 on Fig. 9), as an indication of the range of environmental variables which are represented.

Finally, I urge the authors to make all data publicly available upon publication."

Upon publication, foraminiferal abundance data will be made available. Environmental data is managed by and available upon request from BML and Point Blue.

Minor points: Next to missing on vertical resolution (which likely is not a big problem), the data are affected by the choice of sampling the > 0,150 mm. This means the counts excludes not only juveniles but also adult shells of small species.

This has been added on Page 6, Lines 20.

Taxonomy is not up to date, generic names do not reflect phylogenetic relationships: Turborotalita quinqueloba, Globorotaloides hexagonus, Globigerinella calida, Globigerina bulloides

These have been brought up to date in line with the reviewer's suggestion throughout.

4.1.1 It seems strange to frame the discussion of seasonality in sediment traps by isotopically derived temperatures? The sediment trap data provide direct observations on the seasonality of the flux; there is no need to involve further surrogate variables. If a species has higher flux in winter than in summer then it is a winter species.

Discussion of isotopic results has been removed.

It is unfortunate that the discussion of seasonality and its potential driving factors does not reflect on the review by Jonkers and Kucera (2015). This review presents specific predictions on when during the year the peak fluxes (and thus presumably peak standing stocks) of the four species should occur in the studied region and how strong these peaks should be.

We recognize the importance of this paper in framing the current discussion of foraminiferal seasonality, however, we do not present flux data nor data that is readily comparable to such, as is mentioned briefly in our discussion. Thus, our data cannot speak directly to predictions for temperate species as described in this paper. We can affirm that seasonality in relative abundance is seen in a subset of the species included in the "temperate" group in Jonkers and Kucera (2015), and that some of these are confined to different seasons within our study region with little overlap (G. bulloides and N. pachyderma), and are thus likely to have nonsynchronous flux peaks. This observation will be added to our discussion of seasonality. The findings of Jonkers & Kucera have been briefly acknowledged on Page 16, Lines 21-22 and.

Conclusion of 4.1.1 on N. pachyderma applies specifically to the studied region. N. pachyderma is strongly linked to upwelling (rather than seasonal incursion of cold waters) off Benguela and off Somalia (Ufkes and Zacharias 1993; Ivanova et al., 1993).

Discussion of this has been incorporated in Section 4.2, Page 17, Lines 6-9 as well as in Section 4.3 on Page 19, Lines 14-15.

4.1.3 Line 3: could you please explain how was the significance of the difference established?

This was meant colloquially as opposed to quantitatively and has been removed.

4.1.4 The relationship between calcification and carbonate chemistry is not that simple. There are data indicating opposite trends (more calcification in more undersaturated waters) and there is increasing evidence (see review in Weinkauf et al., 2016) that calcification reflects factors other than carbonate chemistry.

We recognize that this is likely a very complex picture, and have included a wider swath of literature in recognition of this (including Beer et al., 2010, Aldridge et. al., 2012 and Weinkauf et al., 2016). The results of our study do not pertain directly to calcification, which we made no attempt to quantify. We do find it noteworthy that foraminifera are present at low saturation states at which cultured foraminifera show reduced calcification. Very few field studies in foraminifera have looked at populations or calcification at this extremely low saturation state.

4.3. This discussion is only valid, if all N. pachyderma genetic types behave ecologically identically. This is highly unlikely, considering the results presented by Darling et al. (2006, 2007).

This caveat has been addressed on Page 19, Lines 5-7. There are many pitfalls in using foraminifera species alone as environmental indicators, as we briefly note in relation to our findings for *G. bulloides*, this being one of them. In our study region, *N. pachyderma* does appear to be seasonal, and given the good agreement of our finding with those in other regions – at least in association with upwelling "season" in other seasonal upwelling regions and more generally Spring/Summer in most temperature/high latitudes (Jonkers and Kucera, 2015), this may be a good generalization where regional or genotypic specific data may be unavailable.

Table 2: are p-values corrected for multiple hypotheses testing (see Bonferroni correction)? What has been correlated with the environmental variables? Absolute abundance or percentage? Is the use of linear correlation justified? Are the variables normally distributed?

P-values are corrected. Absolute abundance has been correlated with environmental parameters, and all data is normally distributed, with the exception of Fluorescence data, which is somewhat non-normal with a long tail at the high end of values. The exception is foraminiferal abundances themselves with the inclusion of "0" or absent cases.

Figure 2: could the authors indicate the position of the actual CTD casts?

The position of each CTD casts is demarcated by the position of the black point along the upper y-axis and has been added to our figure caption.

Other Document Changes:

Author order has been changed to reflect T.M. Hill as second author.

Page 1, Line 15: “close”

Page 2, Line 6: ~~confirm~~; document

Page 2, Line 13: ~~movement~~; distribution

Page 2, Line 22: Pak et al., 2004 added to references

Page 3, Line 18-20: edited for clarity

Page 4, Line 5: “superimposed on naturally corrosive waters”

Page 4, Line 14: “and calcite”

Page 4, Line 20; ~~pH~~; saturation state

Page 7, Line 5: “(A. Dickson, Scripps Institution of Oceanography, CA, USA)”

Page 7-8; Line 18, 24-1; Edited to reflect additional CCA analysis

Page 10, 11: Lines 21-4 edited to reflect additional CCA analysis

Page 14, Line 18: “biomass and suggestion higher…”

Page 16, Line 22: ~~directly~~; “strongly”

Page 17, Lines 7-19: edited to describe additional CCA analysis

Page 18, Line 2; Venancio et al., 2016 added to references

Page 19, Line 19: ~~contradict~~; “contrast with”

Page 19, Line 20: “North-“

Page 20, Line 3: ~~around~~; “at”

In addition, references and figure numbering have been updated to reflect changes, and some minor spelling corrections have been made.

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.

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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 & Thunnell, 1991), and in the Western Pacific (Eguchi et al., 2003). The majority of this prior work has focused on open-ocean assemblages, however,

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leaving a gap in understanding the seasonal dynamics in coastal upwelling regions, as well as a significant spatial gap within the California Current system between the Southern California Bight and Oregon.

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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, modern nearshore assemblages are of interest because sediments in these regions are among those most likely to contain a preserved carbonate fossil record, and thus intact fossil assembalges, due to the high sedimentation rates and the limitations of a narrow continental shelf above a shallow lysocline.

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Understanding planktic foraminiferal assemblages in coastal upwelling regions is also relevant for predicting future climate and ecosystem perturbations. The California Current and other Eastern Boundary Current upwelling systems have been identified as especially

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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.

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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, 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 from the surface 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 juveniles and small adults, and therefore limited samples to foraminifera of readily identifiable adult developmental stages

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and to species normally included in fossil analyses. Most samples were placed in ambient surface seawater and kept chilled without further preservation to be picked immediately upon return to shore. When this procedure was not feasible, samples were preserved shipboard in 95% ethanol, buffered to a pH > 8.5 with Tris(hydroxymethyl)aminomethane. 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, with *N. incompta* and *N. pachyderma* defined primarily by shell coiling direction (sensu Darling et al., 2006). 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).

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2.3 Environmental Measurements

Water column profiles for temperature, salinity, dissolved O_2 (DO) and fluorescence were obtained across the plankton tow depths using a Seabird Electronics SBE 19 conductivity-temperature-depth (CTD) profiler. Plankton tow nets were equipped with a flow meter for each cast; however, due to frequent failures, flow rates were unreliable and are not 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 analysed spectrophotometrically for pH (total scale) using either a Sunburst SAMI (Submersible Autonomous Moored Instrument) modified for benchtop use (SD +/- 0.009) or an Ocean

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Optics Jaz Spectrophotometer EL200 (SD +/- 0.003) using *m*-cresol purple (Dickson *et al.* 2007). Total alkalinity was determined via automated Gran titration on a Metrohm 809 Titrando (SD +/- 2.809 µmol/kg), with acid concentrations standardized to Dickson certified reference materials (A. Dickson, Scripps Institution of Oceanography, CA, USA). Measurements of pH and alkalinity were carried out at UC Davis Bodega Marine Laboratory and used to calculate other inorganic carbon system parameters, including 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 assumed to be deeper than the profiled water. Upwelling index is taken from the PFEL upwelling index modelled 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).

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2.4 Data Analysis

For the four most abundant species, *G. bulloides, Turborotalia quinqueloba, N. incompta,* and *N. pachyderma,* we performed a CCA (Canonical Correspondence Analysis) on relative abundances using the 'vegan' package in R (R Core Team, 2013; Oksanen, J. et al., 2016). 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. A subset of variables was selected for CCA by exclusion of all variables not related to any total abundances by pairwise correlation at a 95% confidence

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level. Strongly interrelated or redundant parameters were additionally excluded (i.e. a parameter correlated at multiple consecutive depths would have been considered at only one of these depths).

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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.

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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-

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

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 3). *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 increase in relative abundance during the summer at these stations, but remained in low abundance along with *N. incompta* year-round (Fig 4). *T. 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 4).

3.1 Environmental Measurements

In spring and summer, surface hydrographic conditions were highly variable, reflecting alternating upwelling events and relaxation periods. Frequent changes in thermocline depth

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

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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.*

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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* combined with the high summer abundance of *N. pachyderma* creates the appearance of a seasonal switch in the relative abundances of the two Neogloboquadrinids (Fig 3). These trends are described in more detail for each of the four species below.

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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 *N. incompta* and *G. bulloides* reflect 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).

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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 is weak, at best, at the surface. The relationship is slightly stronger at 40 m depth (Fig 7), 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 an increase in *N. pachyderma* in the summer along with cooler temperatures, especially in the sub-surface. 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, occurs mixed with *N. incompta*, whether in the water column or sediment. This pattern is suggestive of an incursion of these cooler, northern waters and not solely the impact of upwelled waters in this region (<10°C conditions).

4.1.2 *Globigerina bulloides*

Globigerina 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 3). 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 (Sutter & 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.

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4.1.3 Spatial Dynamics

Nearshore stations BL1 and BL2 are shoreward from the primary band of coastal upwelling (Huyer, 1983) and show 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 4). 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.

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Short-term spatial dynamics were also observed to impact foraminiferal abundance. On days when overall productivity was low, abundances of all foraminifera species was higher at sites with higher fluorescence (indicating higher biomass and suggesting 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 8). 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

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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 8). 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.

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4.1.4 *Foraminifera in Reduced pH Waters*

Upwelling associated waters with low Ω_{Ca} were observed on multiple occasions during plankton tows. Foraminifera are 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), although this susceptibility may not always manifest through a reduction in shell weight in open ocean conditions (i.e. Beer et al., 2010; Aldridge et al., 2012; Weinkauf et al., 2016). 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 organism 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. However, it is possible that upwelling-adapted *N. pachyderma* may prove to be an example of a calcifying plankton able to tolerate undersaturated waters.

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4.2 Causes of Seasonality and Fluctuations in Abundance

Seasonality has previously been identified in temperate regions globally for all four of the species addressed here (Jonkers & Kucera, 2015). 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 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). This is in slight contrast to the hypothesis of *N. pachyderma* dormancy outside of upwelling season suggested in the Arabian Sea (Ivanova et al., 1999), since in the California Current as well as on the Namibian margin there is some synchronicity between the preferred seasonality of *N. pachyderma* and greater transport into the region from high latitude waters (Fumes & Zachariasse, 1993). An alternation between the foraminiferal fauna of source waters additionally offers an explanation for the seasonal absence and reappearance of both *N. pachyderma* and *G. bulloides*. *N. incompta,* found year-round in the study region, may be present in both water masses.

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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 strongly to single environmental parameters, but rather a suite of hydrographic and temporal variables were required to account for faunal assemblages. For some species, particular variables can be identified through pairwise correlation as having a

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significant effect on abundance (Fig. S2). In *G. bulloides*, higher abundance correlates with higher water temperatures throughout the water column. 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 *T. quinqueloba* is not clearly correlated with any single measured parameter (Fig S2).

A CCA shows the relative abundances of *G. bulloides, N. incompta* and *N. pachyderma* to be dependent upon environmental variables strongly associated with coastal upwelling conditions (Fig 6). However, the directions of those associations vary. *N. pachyderma,* and to a lesser extent, *T. quinqueloba,* seem to be associated with upwelling-like water conditions. Sediment trap time series have previously linked *T. quinqueloba* to productivity in the North Atlantic (Chapman, 2010), which could explain the association of this species with the higher productivity season, although it is not directly associated with shifts in productivity as is *N. pachyderma*. *G. bulloides*, however, is negatively associated with upwelling-like water conditions, and more associated with warmer waters and higher DO levels seen outside of upwelling season. *N. incompta* relative abundances also increase outside of upwelling season, although in this case, relativity may be key, especially with regards to *N. pachyderma* (see 4.1.1). This outcome is supported by total 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, T. 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. 9). Peak counts for each species occur within 7 days of the full moon, before dropping off before

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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; Venancio et al., 2016). 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 artefact of sampling against a background of strong seasonality in a highly variable environment cannot be resolved from this dataset, even though sampling days surrounding the full moon occurred across seasons (Fig 5).

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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 favourable to upwelling. This pattern has been noted along the African margin (Giraudeau, 1993), in the Arabian Sea (Ivanova et al., 1999), and on the Namibian margin (Ufkes & Zachariasse, 1993). It remains possible that other genotypes of *N. pachyderma* have distinct and ecological preferences particularly those associated with the Arctic and Antarctic (Darling et al., 2006; Darling et al., 2007). As our record is based on discrete tows and not a continuous record, the percent

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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 upwelling season 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.

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Globigerina 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 (e.g. 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. The majority (88%) of the *G. bulloides* seen in our samples was observed between November and February. CCA supports these observations in indicating that the relative abundance of this 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.

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5 Conclusions

Surveys of planktic foraminifera retrieved from plankton tows both confirm and contrast with findings of studies in analogous regions. Along the North-Central California shelf there is a clear association between upwelling and *N. pachyderma,* which experiences a summer bloom and increases in relative abundance, as seen at other sites. This summer population of *N. pachyderma* appears to routinely experience low Ω_{Ca} waters, conditions that are predicted to

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increase in the near future. *N. pachyderma* associations 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* at 10.5°. *G. bulloides*, however, is associated in our study with non-upwelled waters, in contrast with populations 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 wealth of information on seasonal-scale processes that is contained within foraminiferal shells. To access this information, however, it is of great importance to ground interpretations of foraminiferal proxies in species and regional ecology to the greatest extent possible.

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Acknowledgements

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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

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

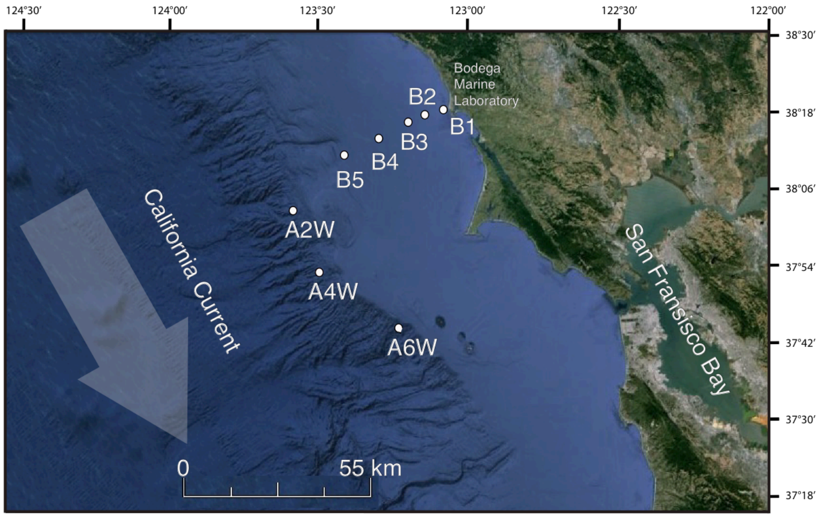

Figure 1. Map of tow stations BL1-5, A2W, A4W and A6W.

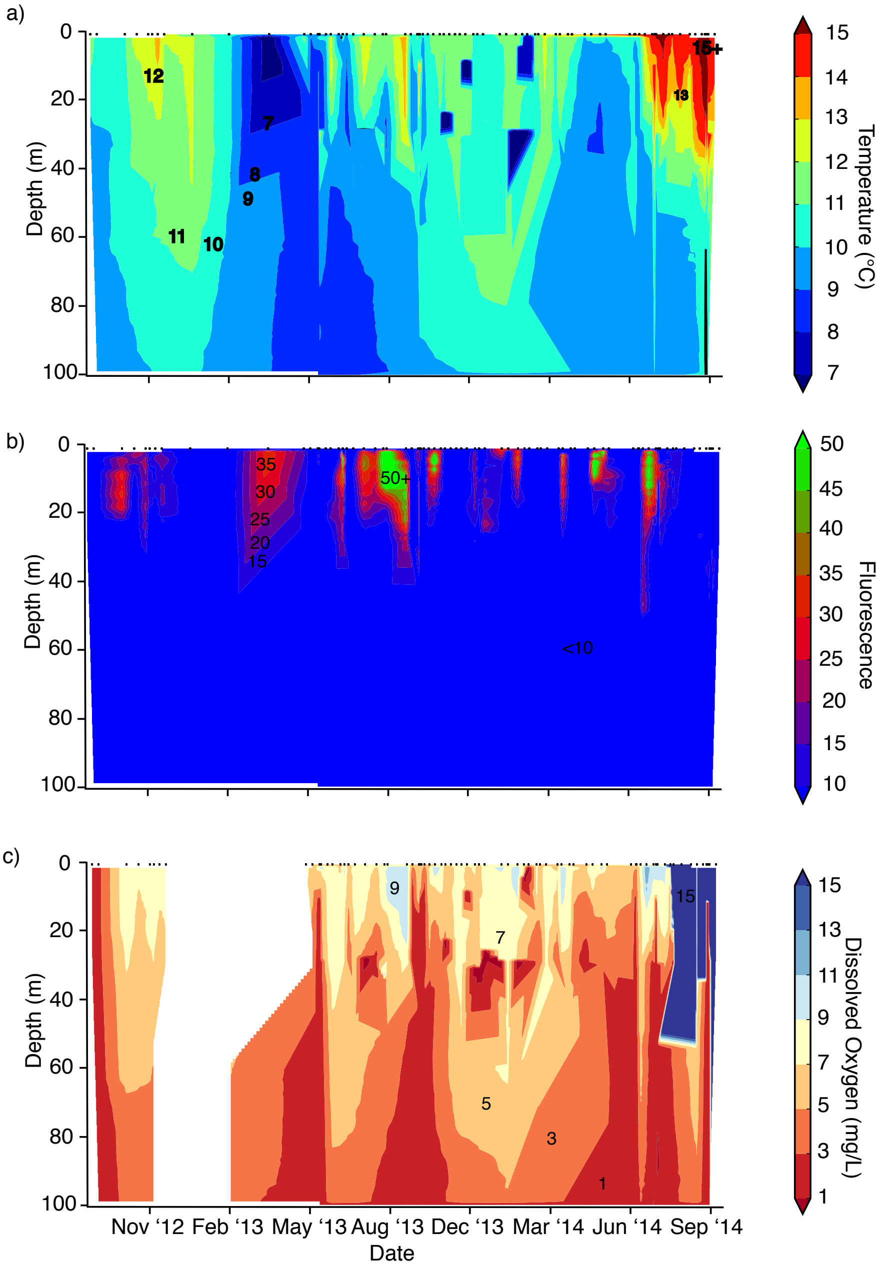

Figure 2. A time-series of CTD cast profiles for a) temperature, b) productivity, and c) DO taken between September 2012 and October 2014. Time-series are compiled from CTD casts

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. Black points at the top of each figure denote the location of each CTD cast.

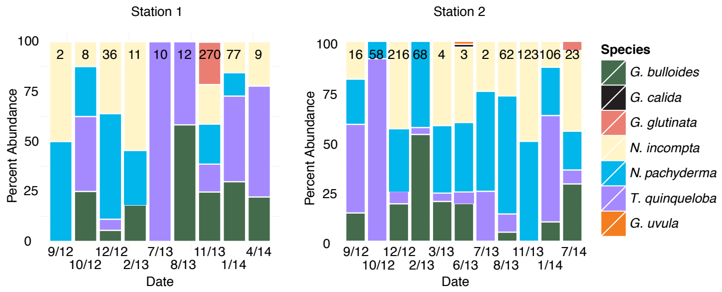

Figure 3. Relative abundance of all species at near shore stations BL1 and BL2, with total number of foraminifera marked at the top of each bar.

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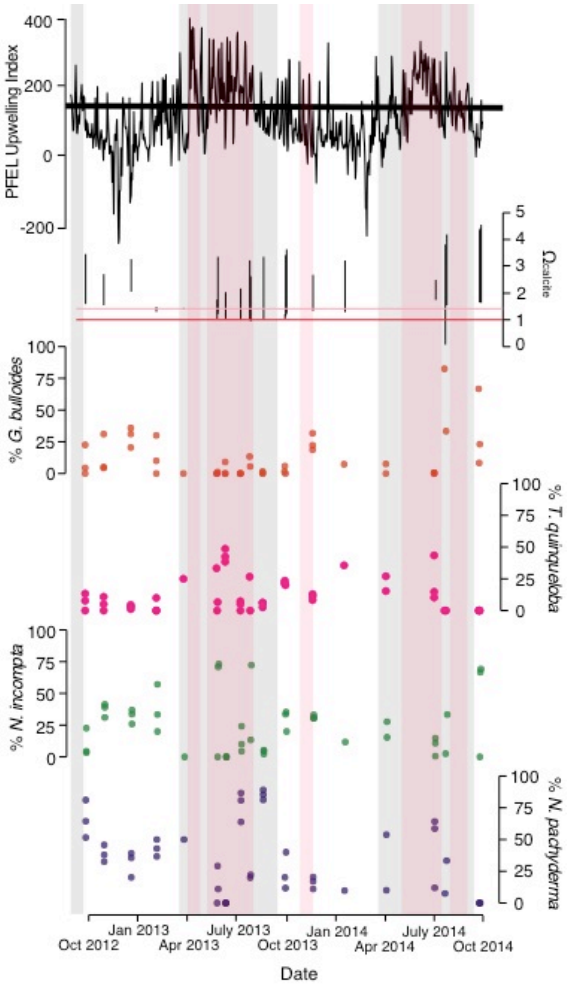

Figure 4. Upwelling index for 39°N (PFEL; http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling.html),), with “upwelling season” shaded in grey, and periods of sustained upwelling conditions during the relevant years shaded in red. The range of C_{alcite} observed on each tow is marked in black, with $\Omega_{calcite} = 1$ marked in red and $\Omega_{calcite} = 1.5$ in pink. Percent abundances from vertical tows of *G. bulloides*, *T. 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.

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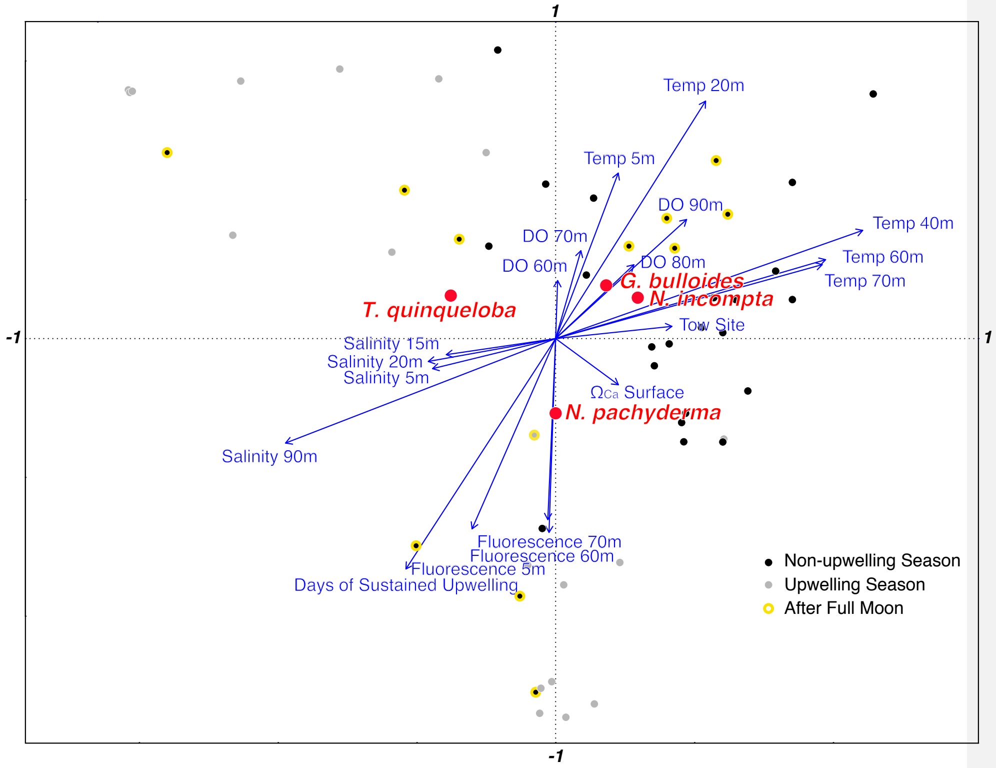

Figure 5. Biplot of Canonical Correspondence Analysis of relative abundance of the four most abundant species compared with environmental variables at the time of collection for all tows in which foraminifera were found. Dominant species are represented by large red points, and small points represent individual tows. Grey points are tows that fall within upwelling season, as shown in Fig. 2, and black points outside of this season. Points with a golden halo represent tows during lunar days 14-18.

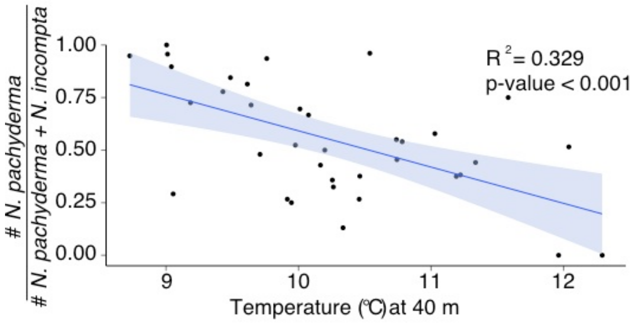

Figure 6. Ratio of *N. pachyderma* to *N. pachyderma* and *N. incompta* at 40m depth with 95% confidence envelopes.

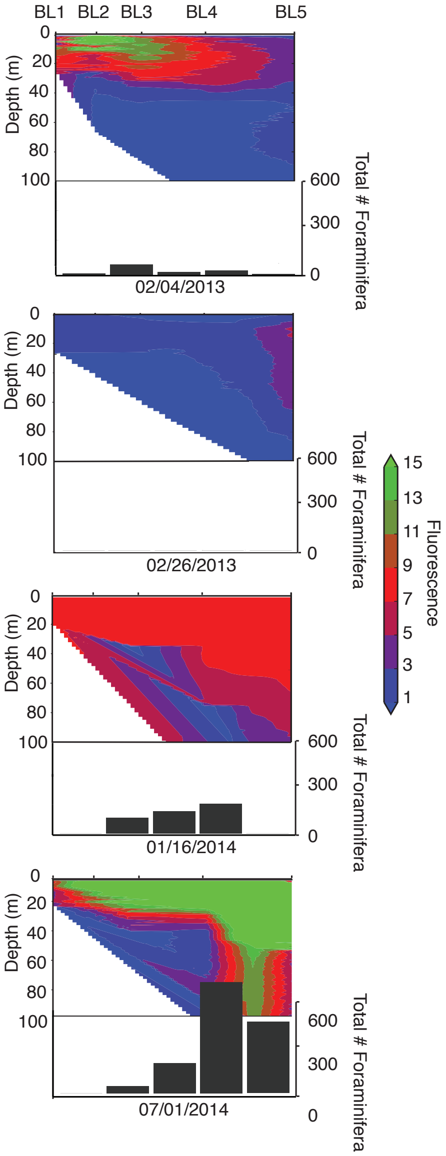

Figure 7. Water column fluorescence data and total number of foraminifera recovered at stations BL 1-5 on four days of extremely low productivity. CTD data from these 5 stations demonstrates small-scale variability from 1 to 32 km offshore along the continental shelf, and compared this with the total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

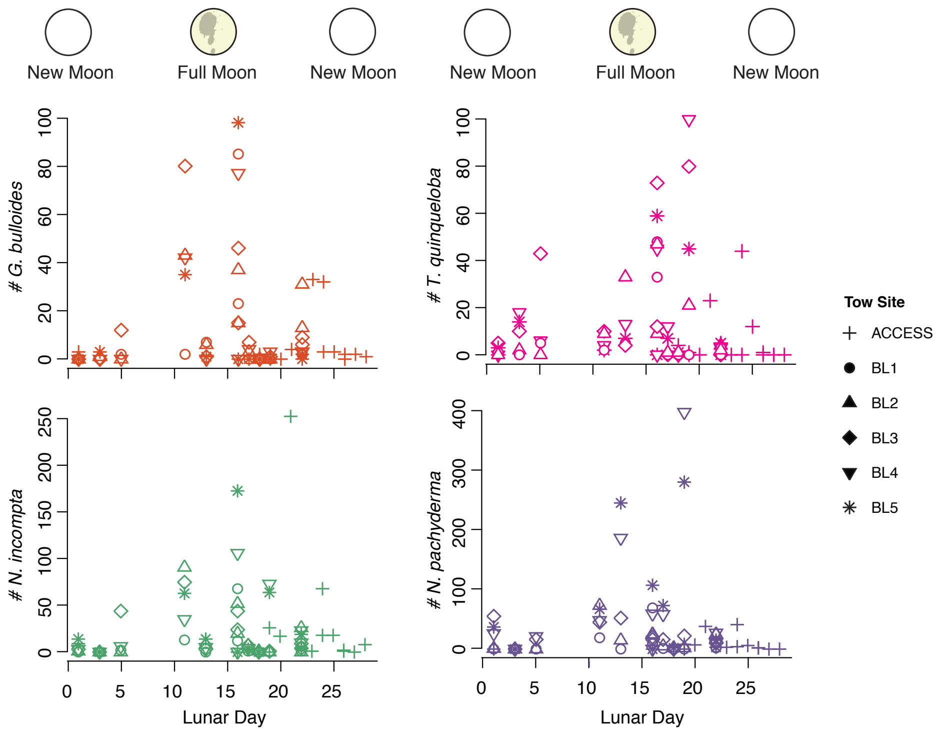

Figure 8. *G. bulloides*, *T*. *quinqueloba*, *N. incompta,* and *N. pachyderma* counts by lunar day from the new moon (Day 0) to Full Moon (Day ~14). Abundances are taken from integrated tows, at 25 m, 45 m, 90 m, 120 m and 200 m depending on the station (see Table 1). Symbols denote tow station.

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