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Dear Jelle,

Please note that the point-by-point response to reviewers and list of relevant changes to the manuscript have already been stated in the author comments published on BGD.net (AC C6596 and AC C6598), which were requested before the submission of a revised manuscript. Enclosed here again are these already published author comments (AC C6596 and AC C6598), which stated our responses to reviewers and how the manuscript would be changed. In addition, and as requested, we have also enclosed a revised manuscript with track changes on how it has been modified in accordance with reviewers' requests.

The manuscript has been revised as stated in AC C6596 and AC C6598, but the page and line numbers for the changes may differ slightly in this revised manuscript, as AC C6596 and AC C6598 were based on the first submitted manuscript (bg-2014-389). In addition, some of the text written in response to reviewer's comments in AC C6596 and AC C6598 has been modified slightly to read better when incorporated into the manuscript.

Please do not hesitate to contact me if you require further information,

Kind Regards,

Kate Salmon.

Response to Anonymous Referee #1

We would like to thank Anonymous reviewer #1 for his/her time and insightful thoughts on our manuscript. Here, we address all the major and minor comments highlighted by reviewer #1. Reviewer's comments are in Arial font and italicised, responses are in Times font, and suggested additions if necessary are in bold, italic Times font within inverted commas:

1. *"In the introduction the authors ………. Nevertheless, when attempting to explain what drives the variability in the fluxes they ignore this species-specific behaviour and only describe the total PF flux. This needs to be addressed. At the minimum the authors need to discuss the different patterns in the three groups of species they distinguish (surface, intermediate and deep dwellers), but ideally they also attempt to explain what drives the differences between the individual species in these groups"*

The citation of Kuroyanagi and Kawahata (2004) in its current form is perhaps a bit misleading considering we do not concentrate on species-specific responses in this paper. We propose to remove the species-specific comment in Section 1, page 12225, line 16: "***in addition, different environmental variables may induce species-specific responses (Kuroyanagi and Kawahata (2004)***"

We agree with the reviewer that the species-specific variability is interesting as we observe in section 4.2, page 12231, lines 12-15. However, for a detailed discussion of seasonal species-specific variability and assemblage shifts at this site, the remaining 15 species present need to be taken into account. Such a detailed study is ongoing by Prof. Warren Prell at Brown University from the 3200m-depth trap, which will include our overlapping species-specific data (for 11 PF species) from the shallower trap. This combined long-term data from two different depths will be published separately and would make a more comprehensive comparison with previous time-series work from same location.

We deliberately wanted to focus on what causes interannual changes in total PF flux as a whole in this specific manuscript because it better describes the overall biological response to distinct oceanographic features such as eddies. Seasonal variations in PF species have been extensively studied at this site (Fairbanks et al.,1980, Deuser et al. 1981, Deuser 1987, Deuser and Ross 1989 and Tolderlund and Bé 1971) and flux changes in groups of PF species have been previously linked to phytoplankton succession here and at other sites (Tolderlund and Bé 1971, Thunell and Reynolds, 1984, Deuser and Ross 1989, Sautter and Thunell, 1989) so we found it unnecessary to include a separate discussion on individual species groups and instead focus our study on an interannual-based total PF flux which makes a unique and perhaps valuable contrast to the species-specific seasonal-based studies previously published.

For current purposes, we hope that figures 4-6 show readers how the species selected for this study relate to one another on a seasonal and interannual timescale (species studied= 11 and total PF species present= 26). In addition, we have added a brief discussion of surface dweller variability in contrast to deeper dweller variability in answer to comment 4.

2. *"Moreover, the division into the groups in terms of depth habitat is in this respect perhaps not the most useful and the authors may want to divide the species into groups that share similar shell flux patterns."*

In general, we observe that the depth-habitat grouping also tends to describe similar flux patterns, but will be willing to change "***Figures 4-6"*** according to the similar flux patterns as below, if essential:

"Group 1: *G. ruber* (white and pink), *G. sacculifer*
Group 2: *N. dutertrei, G. siphonifera O. universa*
Group 3: *P. obliquiloculata, G. truncatulinoides, G. hirsuta, G. crassaformis, G. inflata"*

3. *"When it comes to the species specific flux patterns, the difference between the timing of the peak flux of the deeper dwellers is interesting and something the authors point out, but do not discuss"*

We agree with the reviewer that it is interesting that *G. truncatulinoides* flux peaks before other deeper dwelling species. We will add the following text to section 5.1.1, page 12233, line 2:

"from the spring phytoplankton bloom (Hemleben et al. 1989). ***The discrepancy in timing of peaks between the deeper dwellers (Figure 7) is likely due to subtle changes in food availability and diet of species and phytoplankton succession (Deuser and Ross, 1989, Hemleben et al. 1989). Overall, the seasonal PF species succession is broadly similar to previous observations from 1959-63 and 1978-84 (Tolderlund and Bé, 1971, Deuser 1987, Deuser and Ross, 1989) which suggests that despite long-term environmental change, there has been no significant shift in species seasonality and environmental controls have remained consistent over the past 50 years."***

As mentioned above in response to comment 1, we hope to explore these relationships in more detail with long-term species seasonality data set in a separate manuscript.

4. *"Similarly, there seem to be clear changes in variability in the flux between years for several species (G. sacculifer, G. ruber (white) and G. siphonifera) and (surprisingly) apparent absence of seasonal variability in some surface dwellers (large changes in temperature and other environmental parameters)."*

We suggest the interannual changes in surface dwellers may be due to the relatively 'stable' environmental variables prevalent within an oligotrophic subtropical gyre. For instance, the thermal tolerance of the surface-dwelling species are never exceeded throughout the ~8ºC seasonal surface temperature changes at BATS and the nutrient content of the upper mixed layer is almost always negligible. In addition, their shorter lifecycles (~couple of weeks compared to months for deeper dwellers) suggests they may be more adaptable to environmental changes in the surface ocean and therefore their fluxes may reflect more environmental noise when compared to deeper-dwelling species.

As we mentioned in response to comment 1 above, species-specific seasonal and interannual responses will be described in detail in a different manuscript but we will add a brief explanation on the interannual flux changes in the surface dwellers, section, 5.1.1, page 12233, line 5:

"…and the export flux of phytodetritus to depth. ***The surface-dwelling symbiont-bearing foraminifera have lifecycles which benefit from strongly stratified surface waters in order to photosynthesise so they can succeed in low nutrient conditions (Hemleben et al. 1989) and do not bloom when the mixed layer is deepest. Surface dwellers generally bloom in late summer when sea surface temperatures are at a maximum and dinoflagellates are abundant (Tolderlund and Bé, 1971).*** We thus conclude that the depth of the mixed layer plays an important role in regulating PF flux….."

5. *"I find this section of the manuscript (5.1.1 and 5.1.2) difficult to understand, or rather, difficult to understand the mechanisms that would underlie the observed relationships. At the beginning of the authors mention observations from the high latitudes that show a relation between MLD deepening rate and deepening timing and productivity. Subsequently the deepening rate and its potential influence on PFF is discussed and another parameter (shoaling rate) is introduced, but the timing of the MLD deepening is not discussed. I find this confusing and have several comments on this section: First of all, the mechanism the authors use to explain how MLD can exert an influence on the PFF is indirect and via export productivity, which they derive from surface chl-a concentrations and carbon fluxes at different depths. Since the authors state that the foraminifera rely on the organic matter flux from the surface ocean for food (and hence growth and hence flux), it would make sense to explore this relation first and then focus on the relations between OM export and MLD dynamics. The relation between PFF and MLD is only indirect and correlations between PFF and MLD could therefore be misleading."*

We only acknowledge the fact that the seasonal flux in export fluxes of organic carbon may fuel PF production in section 5.1.1, page 12232, section 5.1.1, line 19.

However, we realise that export fluxes of organic carbon will only benefit the symbiont-barren foraminifera with herbivorous diets, in particular deeper dwelling foraminifera. Therefore, Chlorophyll *a* is a much more inclusive indicator for foraminifera food concentration; it is generally correlated with copepods, a prey of spinose foraminifera (*O. universa, G. ruber, G. sacculifer,* Hembleben et al. 1989), and non-spinose foraminifera with herbivorous or detritivorous diets generally feed on prey which contain chlorophyll *a* (Lombard et al. 2011). It therefore follows that environmental controls on Chlorophyll *a* should also control the abundance of planktonic foraminifera (if not light-limited, and within thermally favourable conditions- Ortiz et al. 1995). There may be some light-limitation at this site as suggested by Lombard et al. 2009 but there was not enough data to confirm this during their study. Our findings are consistent with other PF flux studies where seasonal changes in the mixed layer depth and associated changes in chlorophyll *a* concentrations show strong association to seasonal changes in species fluxes (King and Howard, 2003, Thunell and Reynolds, 1984).

We will change section 5.1.1, Page 12232, line 17 to clarify this (changes in bold italic):

"Here, we also observed a simultaneous seasonal peak in chlorophyll a and maximum depth of the MLD ***as seen by previous studies at BATS (Cianca et al. 2012)***, the timing and amplitude of which coincides with the maximum PF flux (Fig. 2c and d). ***This observation is consistent with previous findings in other ocean basins where seasonal changes in mixed layer depth are closely associated with changes in foraminifera production (Thunell and Reynolds, 1984, Sautter and Thunell, 1989, Pujol and Vergnaud Grazzini 1995, Schmuker and Sciebel 2002) and chlorophyll a concentrations (King and Howard, 2003, 2005). Siegel et al. (2002) proposed that south of 40°N, the initiation and extent of the spring bloom is dominantly limited by nutrients rather than light, and this is supported by the simultaneous increase in phytoplankton concentrations with mixing depth at BATS (Treusch et al. 2012***). Vertical mixing in late winter and spring distribute nutrients into the euphotic zone to support the spring phytoplankton bloom ***which fuels foraminifera production***, as indicated by the seasonal peak in export fluxes of organic carbon (Fig. 1d)*"*

6. *"Secondly, while the observed relationships the authors identify in Fig. 9 are statistically convincing, I struggle to grasp what the actual mechanism(s) explaining these observation is (are). Does it mean that the spring bloom has always approximately the same length (relation between Dr and MLD)?"*

In this study, the seasonal peak in PF flux is always of approximately the same length. The spring bloom only starts when the MLD penetrates the nitricline and deep chlorophyll maximum which lies at 80-100m at this site. The MLD starts to deepen with increased wind stress and decreased heat flux at the surface and this can vary due to changes in the North Atlantic Oscillation (NAO). For instance, winter 2009 experienced the deepest MLD (and fastest deepening rate) driven by the negative NAO causing increased wind stress and convective mixing. However, slower deepening rates such as in 2007-2008, led to the formation of a shallow mixed layer depth. The deepening rate is controlled by wind forcing and heat fluxes in the surface ocean and thus it primarily reflects the maximum depth reached by the mixed layer and therefore concentration of nutrients entrained into the euphotic zone and consequent size of the following spring bloom. We will re-write section 5.1.2. to incorporate this explanation.

7. *And if Sr has a major influence on productivity and PFF why do fluxes increase when conditions are changing to less optimal conditions (stratification) more rapidly?*

There are potentially two factors, which could control the size of the phytoplankton spring bloom at BATS and therefore the food availability for PF that we will clarify in section 5.1.2, page 12233.

1. The dominant control is the depth of the mixed layer (determined by the strength of convective mixing reflected in the deepening rate)
2. There is some evidence that light availability could be a secondary, weaker control (Dutkiewicz et al. 2001, Cianca et al. 2012, Lomas et al, 2009) as the euphotic zone at this site lies ~100m (Steinberg et al. 2001).

The shoaling rate reflects the rate at which the nutrients mixed in the water column are entrained to the surface where they can be utilised by phytoplankton, which require light to bloom. A faster shoaling rate will also concentrate the food for foraminifera in the euphotic zone, producing a shorter and sharper bloom, as mentioned in section 5.1.2, page 12233, line 11, or as we see here, a larger bloom. Years with quicker shoaling rates (1998-99 and 2009-10), have greater fluxes of thermocline dwelling species such as *N. dutertrei, P. oblquiloculata, G. siphonifera*, and in 2009-10, *O. universa* suggesting that during higher rates of shoaling, the seasonal thermocline is nearer to the surface which is beneficial for these symbiont-bearing and symbiont-facultative species. We will re-write section 5.1.2. to incorporate this explanation.

8. *"This needs more explanation and the authors need to be clear about whether it is absolute MLD, Dr, Sr, or their ratio (or something else) that controls the PFF (see also P12233, L28 and beyond where in one year the large flux is suggested to be related to Dr and MLD and in another year only to MLD, whereas in Fig. 9 and on P12233, L 21-23 PFF is said to depend on the Dr/Sr, which mainly reflects the Sr)."*

We have re-written section 5.1.2, page 12233-34 discussing the explanations written above and will alter references to the D_r/S_r to just discussing the shoaling and deepening rates in this section of the text. We will more fully describe the controls of deepening and shoaling rate and how this relates to the depth of the mixed layer by including some of the explanations in answers to comments 6-7.

9. *"1. What is the basis of the 80m limit used to determine the relation between MLD and PFF? It seems arbitrary. "*

The '80m' limit corresponds to the Deep Chlorophyll Maximum Layer (DCLM), where many species of PF reside in association with other zooplankton (Fairbanks and Wiebe, 1980) is ≥ 80m for the majority of the year (Steinberg et al. 2001). This is supported by Treusch et al. 2012, who found that the DCML developed between 80-120m during the summer stratification period. In addition, Steinberg et al. 2001 found that deeper mixed layers (>100m) are associated with higher chlorophyll *a* values. >80m is also the depth horizon at which the nitrate concentrations exceed 0.1 umol/kg which defines the nitricline (Sciebel et al. 2001) (see page 12232, line 22).

This means that unless the mixed layer penetrates at least 80m, then access to the food supply for PF is limited and this is why we see a correlation in Figure 3c.

We will add the following to section 5.1.1, Page 12232, line 21:

“ In contrast, there is no correlation during the late spring to autumn when the MLD is less than ~80m (Fig. 3d), ***the minimum depth of the deep chlorophyll maximum layer where many species of planktonic foraminifera reside in association with other zooplankton and algal cells (Fairbanks and Wiebe, 1980). During summertime, the mixed layer fails to penetrate this layer also known as the nitricline (defined as nitrate concentrations > 0.1 umol kg^{-1} ”***

10. *“2. The shoaling rate in year 2000 represents only a minimum value since there is a month missing during the decrease of the MLD. This could affect the results of the regression. “*

This is true. We will omit this value from the regression and in Table 2.

11. *“3. The deepening rate is defined as the average of the rate between Oct and Jan. Why this interval and not the average rate over the entire period of MLD deepening (which extends beyond Jan)?”*

The deepening rate used in Table 2 does in fact represent the entire period of deepening regardless of the month. This will be re-written on Section 5.1.2, page 12233, line 13:

“At our subtropical study site, the mean rate of deepening of the mixed layer is strongly correlated to the maximum MLD reached ($r^2 = 0.88$)”

12. *“4. How are the start and end of the spring bloom period defined? And therefore the average winter-spring flux? This needs to be done objectively in order to compare different years.*

Currently the spring bloom and winter-spring flux varies in its start, length and end point each year but is always within approximately the same 6-month period (end of November to April). The spring bloom average here was calculated based on the time when the PF flux began to first increase dramatically (which varies year to year, see table below). We therefore calculated the duration of the bloom and the average flux based the table below:

Year of bloom	**Month of bloom 'start'**	**Month of bloom 'finish'**
1998	February	April
1999	February	April
2000	January	April
2008	December	February
2009	December	March
2010	January	March (but continued to May due to eddy interference)

We make each year comparable by integrating the total PF flux over the spring bloom so it is independent of the start, finish and duration of the bloom.

13. *And in addition, wouldn't the integrated flux be a better parameter to investigate?"*

We do use integrated flux - we will change the legend in Table 2 to describe this as 'integrated winter-spring PF flux' and on the y-axis labels on figures 9b and 9d.

14. *"5. What is the physical reason the fit a logarithmic curve to the data in Fig. 9D? Would one expect such a relationship with decreased sensitivity at faster rates?"*

There is no physical mechanism to explain why higher rates of shoaling should cause lower sensitivities of the PF flux. The logarithmic relationship was simply applied to include an anomalously quick shoaling rate in spring 1999 (Table 2). We will apply a linear relationship in Figure 9D.

15. *“The suggestion that eddies can under certain circumstances prolong and/or enhance primary productivity and PFF is very interesting. Discussing what these circumstances are exactly would contribute to the quality of the paper. There are several times when the passing of an eddy did not have an effect on the PFF (e.g. winter 98/99, 07/08). Where they too early? Or were other conditions not met?”*

We will put our findings on eddies into more context with other observations of PF flux changes within eddies in section 5.2, page 12234, line 12 (changes in bold italic):

The negative sea level anomalies in spring 2009 and 2010 indicate that the large (and in 2010 prolonged) PF fluxes in these years are clearly associated with the passage of cyclonic eddies (Fig 2b). ***Eddy pumping of nitrate into the euphotic zone has been extensively studied at BATS and shown to significantly increase new production (Oschlies and Garçon, 1998) although estimates of eddy nitrate contribution range from*** ~30-70% in the Sargasso Sea. ***The upwelling/downwelling of nutrients by cyclonic/anticyclonic eddies have been shown to either*** promote ***or suppress*** phytoplankton blooms (Eden et al., 2009; Goldthwait and Steinberg, 2008; McGillicuddy et al., 1998, 1999, 2007; Sweeney et al., 2003; McGillicuddy and Robinson, 1997, ***Lomas et al. 2013, Cianca et al. 2012***) and ***therefore affect the PF food source (Schmuker and Schiebel, 2002). In addition, eddy pumping may vary on decadal timescales in concert with NAO changes as suggested by Cianca et al. 2007. Previous studies have found higher fluxes of certain PF species such as Globigerinita glutinata associated with cyclonic eddy structures in the Caribbean Sea (Schmuker and Schiebel, 2002), North Atlantic (Beckman et al. 1987), in conjunction with upwelling frontal regions in the Mexican Pacific (Machain-Castillo et al. 2008) and deep mixed layers during winter in the Mediterranean (Pujol and Vergnaud Grazzini, 1995). We see a similar response in our record in spring 2009 particularly for deeper dwelling species, which was the largest PF flux observed over the entire record, even though the maximum MLD was modest, and the average rates of mixed layer deepening and shoaling were similar to lower flux years (Table 2).***

And in Section 5.2, page 12235, line 4:

…during the seasonal flux of deeper dwellers (Fig. 6). ***This observation is in agreement with findings from the Eastern Basin of the Mediterranean where greater numbers of grazing species such as G. truncatulinoides and G. inflata are found in association with numerous eddy structures and deep mixed layers (Pujol and Vergnaud Grazzini, 1995). These findings suggest that cyclonic eddies enhance the abundance of deeper dwelling species through aiding their annual reproductive migration through mixing of the water column in addition to driving large carbon export flux.***

Section 5.2, page 12235, line 8:

Occurrence of cyclonic eddies synchronous with deep MLDs act to enhance the existing seasonal cycle of certain PF species associated with mixed water columns by increasing cyclonic mixing, and therefore chlorophyll concentrations and organic carbon flux. From our results, we observe no biological response when cyclonic eddies do not occur synchronously with deep MLDs, such as in winter 2007-08 when the mixed layer barely penetrated the nitricline. This suggests that the extent of the spring bloom and PF flux is dominantly controlled by the mixed layer dynamics and cyclonic eddies act to enhance this existing seasonal cycle. For instance, spring 2010 experienced the deepest mixed layer observed during the entire BATS time series (Lomas et al. 2013), enhanced by a cyclonic eddy. Our observations also suggest that eddies need to be present for a minimum of 1 month to elicit responses in PF which have minimum lifecycles of two weeks. For instance, in winter 1998-99 a cyclonic eddy passed over the sediment trap site in only one month but elicited no biological response, compared to cyclonic eddies in 2009 and 2010, which both remained over the site for a minimum of 2-3 months and elicited large biological responses. Similarly, recent studies have found that biological responses differ depending on the type and age of the eddy (Mouriño-Carballido and McGillicuddy, 2006) and eddies that are a minimum of 1-2 months old are more likely to induce a larger biological response (Sweeny et al. 2003). In our record, spring 2010 experienced the deepest mixed layer observed during the entire BATS time series (Lomas et al. 2013), when the deepest MLD and fast shoaling rate was combined with a particularly negative NAO index and a large cyclonic eddy ***which remained at the trap site for up to 3 months***. ***The deep MLD and fast shoaling rate during spring 2010 caused elevated chlorophyll a***

concentrations in the surface 25m (Figure 2d) and the following cyclonic eddy caused a large peak in chlorophyll a concentrations at 80-100m (the level of the deep chlorophyll maximum), similar to elevated subsurface chlorophyll a concentrations following a cyclonic eddy observed by Cianca et al. 2007. These conditions prolonged the PF flux and all other mass fluxes in 2010 (Figure 1)**.**

16. *It is interesting that the eddy in 2010 seems to be associated with increased PFF and organic carbon fluxes, but not with higher chl-a (i.e. no bloom?). Could this perhaps point to lateral advection of foraminifera or of organic matter (which would fuel foraminifera growth without requiring an increase in primary productivity) within the eddy?"*

Although the concentrations in the surface (0-25m) chlorophyll *a* are not elevated, the subsurface chlorophyll *a* concentrations within the province of the deep chlorophyll maximum and nitricline (80-100m) are the highest recorded at BATS since 1990. This is similar to observations of eddies made by Cianca et al. 2007 who found elevation of chlorophyll *a* and nutrients at 100m during a cyclonic eddy in the Eastern North Atlantic. This increase in primary productivity during spring 2010 is also supported by the high, prolonged fluxes of all the mass fluxes (Figure 1).

We will change Section 5.2, page 12235, line 10 (as stated in answer to comment 15):

The deep MLD and fast shoaling rate during spring 2010 caused elevated chlorophyll a concentrations at the surface (Figure 2d) and the following cyclonic eddy caused a large peak in chlorophyll a concentrations at 80-100m (the level of the deep chlorophyll maximum), similar to elevated subsurface chlorophyll a concentrations following a cyclonic eddy as observed by Cianca et al. 2007. These conditions prolonged the PF flux and all other mass fluxes (Figure 1)**.**

The increased subsurface Chl *a* suggests that the cyclonic eddy caused an isopycnal uplift which increased primary productivity to drive the sustained PF flux, rather than lateral advection of the foraminifera population. This corresponds to increases in thermocline species such as *O. universa* coincident with the subsurface Chl *a* peak. This argues against a PF population being laterally advected independent of any primary productivity increase, although we do acknowledge that eddies could provide a mechanism to transport foraminifera in other instances.

17. *The influence of the NAO: "The suggested link with NAO is very interesting. It is based on two years with positive- neutral NAO and one year of negative NAO. Of the years of positive/neutral NAO one is from a trap more than 1500m further down and it has often been shown that PFF recorded at different depths can differ significantly. Therefore the suggestion that NAO might have an influence on the PFF is effectively based on only two years of observations (what about the other years in this study? How do they relate to NAO?)""*

We will add a new figure 10 incorporating all PF flux from this study and Deuser, (1987), Deuser and Ross, (1989) (NAO vs. PF flux) and rewrite section 6, page 12236, line 6:

"To test this, ***we compare PF fluxes covering a range in NAO indexes, from this study using the 1500m sediment trap to those made by Deuser and Ross, (1989) between 1978-84 using the 3200m sediment trap. Despite comparing traps from different depths, the annual integrated PF fluxes are comparable and all are plotted in Figure 10 against the wintertime (DJFM) NAO index, the months coinciding with the period of maximum PF flux. In this comparison, the wintertime NAO index from the previous year (before the PF flux) was used because there is likely to be a time lag of between 6-12 months before the ocean responds to atmospheric forcing (Bates, 2001, 2007, Cianca et al. 2012). Generally PF fluxes are higher during negative NAO phases and lower during positive phases, consistent with correlations between NAO and chlorophyll a variability (Lomas et al. 2010) and MLD (Bates, 2012). The regression in Figure 10 does not include the year 1978-79 because the NAO index for February 1978 is skewed towards an anomalously negative sign in February, despite a positive sign in January and March. The PF flux may not have responded as expected in 1978 due to a shallow MLD or even an anticyclonic eddy which can suppress the spring bloom and hence PF flux, as seen in 1994 at BATS by Lomas et al. (2013). Furthermore, we find on average a 28% reduction in PF flux in NAO positive compared to NAO negative years ($p < 0.025$), when combining PF flux data with those from 1979-84 in Deuser and Ross (1989).***"

*NAO data available from http://www.cpc.ncep.noaa.gov/data/teledoc/nao.shtml

18. *"While it is an interesting suggestion that the NAO can have an influence on the PFF and therefore on the C-pump I think it's only that: a suggestion and the conclusions should be toned down accordingly (also in abstract)."*

We would be happy to include figure 10 (NAO vs. PF flux) to strengthen the implications section (section 6, page 12236) but include a statement to acknowledge the limitation of the dataset such as on page 12236, section 6:

"***We do recognise that the data set used in this example is limited and a more flux data collected over a longer time period is needed to fully test the observed decadal changes between NAO and PF flux."***

And on page 12237, section 7, line 22:

*"*Our findings suggest that the North Atlantic Oscillation, via its influence on mixed layer depth, ***eddy pumping and nutrient upwelling could act to modulate the total PF flux*** and the foraminiferal component of the carbonate pump in the subtropical North Atlantic on decadal timescales. ***However, this finding is only based on 8 years of PF flux data and a much longer-term dataset will be needed to fully understand if the NAO can modulate the PF flux on decadal timescales."***

19. The shell flux data should be made available, either as a table in the paper or through an on-line database such as Pangaea.de.

Yes, this will be done (available from Pangeaa.de after acceptance)

20. P12224, L2: oligotrophic regions are by definition nutrient poor.

Changed

21. P12226, L20: warm temperatures should be high temperatures and similarly cold should be low. Please change throughout the manuscript.

Changed

22. P12229, L9-16: this should be part of the paragraph describing the OFP time-series (3.1).

This section has been added to Section 3.1, page 12228, line 22.

23. P12229, L19: perhaps change ‘relative’ to ‘in relation’?

Done.

24. P12229, L24: ‘deep spring fluxes’ is not clear.

We have changed ‘deep spring fluxes’ to ‘spring mass fluxes’.

25. P12231, L20: t is not clear that the timing of the maximum is really later. I suspect that given the inter-annual variability this difference is insignificant.

We have changed section 4.2, page 12231, line 18 to read:

G. truncatulinoides is then followed by *G. hirsuta, G. crassaformis* ***and G. inflata which all peak between March and April.***

26. P12234, L11: mesoscale eddies are also an environmental control on the PF, the §should therefore be 5.1.3.

Changed to 5.1.3.

27. Fig. 2: please be consistent in the use of symbols for the parameters other then PF.

Fig. 2 c,d,e have all been changed to the same symbol

28. Fig. 3c,d: what is the criterion for splitting at 80m?

Please see response to Comment 9.

29. Fig. 4-6: please add SST curve to graphs to provide clearer information about when the peaks occurred. There is no gap in the time-series of G. sacculifer in Fig. 4.

Done.

30. Fig. 7: place G. crassaformis on its own axis to show the variability.

Done.

31. Fig. 9c: I assume that the extreme chl-a datum has been excluded from the regression. Please indicate this clearly.

Done.

New References

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Response to Anonymous Referee #2

We would like to thank anonymous reviewer #2 for his/her time and insightful thoughts on our manuscript. We would like to stress here again that the main focus of this manuscript is to describe the interannual variability of the total PF flux and discuss reasons for such variability. As mentioned in the response to the reviewer #1 comment, we cannot make detailed comments on the seasonal variability in PF species flux because our dataset does not represent all PF species but our PF species flux (11 species) will be combined with another long term overlapping time-series study [Prof. W. Prell] with a view to achieving this goal. Here we would like to address all comments and will revise the manuscript by incorporating other suggested changes. Reviewer's comments are in Arial font and italicised, responses are in Times font, and suggested additions if necessary are in bold, italic Times font within inverted commas:

1. *"In general the paper is concise, well written, clear and well-focused on the Bermuda. The latter, however is also a limitation as similar studies from elsewhere are not included in the discussion of results, which would increase the value of this study, e.g. with respect to both seasonality and eddy perturbation."*

We have not discussed species seasonality specifically in the discussion of the results because our manuscript is focusing on interannual variability (also see response to reviewer #1 comments).

We are happy to add some more discussion within this context in section 5.1.1 and section 5.2 taking into consideration other global studies on total PF flux variability, as below:

(Interannual variability) Section 5.1.1, Page 12232, line 17 (changes in bold italic):

"Here, we also observed a simultaneous seasonal peak in chlorophyll a and maximum depth of the MLD ***as seen by previous studies at BATS (Cianca et al. 2012)***, the timing and amplitude of which coincides with the maximum PF flux (Fig. 2c and d). ***This observation is consistent with previous findings in other oceans***

where seasonal changes in mixed layer depth are closely associated with changes in foraminifera production (Thunell and Reynolds, 1984, Sautter and Thunell, 1989, Pujol and Vergnaud Grazzini 1995, Schmucker and Sciebel 2002) and chlorophyll a concentrations (King and Howard, 2003, 2005). Siegel et al. 2002 proposed that south of 40^{o}N, the initiation and extent of the spring bloom is limited by nutrients rather than light, and this is supported by the simultaneous increase in phytoplankton concentrations with mixing depth at BATS (Treusch et al. 2012). Vertical mixing in late winter and spring distribute nutrients into the euphotic zone to support the spring phytoplankton bloom ***which fuels foraminifera production***, as indicated by the seasonal peak in export fluxes of organic carbon (Fig. 1d)***"***

(Eddy perturbation) Section 5.2, page 12234, line 12:

"The negative sea level anomalies in spring 2009 and 2010 indicate that the large (and in 2010 prolonged) PF fluxes in these years are clearly associated with the passage of cyclonic eddies (Fig 2b). ***Eddy pumping of nitrate into the euphotic zone has been extensively studied at BATS and shown to significantly increase new production (Oschlies and Garçon, 1998) although estimates of eddy nitrate contribution range from*** ~30-70% in the Sargasso Sea. ***The upwelling/downwelling of nutrients by cyclonic/anticyclonic eddies have been shown to either*** promote ***or suppress*** phytoplankton blooms (Eden et al., 2009; Goldthwait and Steinberg, 2008; McGillicuddy et al., 1998, 1999, 2007; Sweeney et al., 2003; McGillicuddy and Robinson, 1997, ***Lomas et al. 2013, Cianca et al. 2012***) and ***therefore affect the food source of planktonic foraminifera (Schmuker and Schiebel, 2002). Previous studies have found higher fluxes of certain PF species such as Globigerinita glutinata associated with cyclonic eddy structures in the Caribbean Sea (Schmuker and Schiebel, 2002), North Atlantic (Beckman et al. 1987), in conjunction with upwelling frontal regions in the Mexican Pacific (Machain-Castillo et al. 2008) and deep mixed layers during winter in the Mediterranean (Pujol and Vergnaud Grazzini, 1995). We see a similar response in our record in spring 2009, which was the largest PF flux observed over the entire record, even though the maximum MLD was modest, and the average rates of mixed layer deepening and shoaling were similar to lower flux years (Table 2)."***

(Eddy perturbation) Section 5.2, page 12235, line 4

"···during the seasonal flux of deeper dwellers (Fig. 6). ***This observation is in agreement with findings from the eastern Basin of the Mediterranean where greater numbers of grazing species such as G. truncatulinoides and G. inflata are found in association with numerous eddy structures and deep mixed layers (Pujol and Vergnaud Grazzini, 1995). These findings suggest that cyclonic eddies enhance the abundance of deeper dwelling species through aiding their annual reproductive migration through mixing of the water column in addition to driving large carbon export flux."***

2. *"Having said that, the manuscript is well within the scope of BG, presents novel data and discusses these data in a broader oceanographic perspective. The manuscript would benefit from the addition of a map showing the location of the site with major surface currents, as well as with a full data table (supplementary).*"

We will add a map without surface currents, as there are not significant boundary currents or fronts present at this site. We will include all data in Pangeea.de (also see our response to reviewer #1).

3. *"Materials and Methods, 3.2, line 15-16: The authors state that the fast settling rates for individual tests of larger species would not cause a temporal offset between the hydrography and their arrival at 1500m depth (3 days for G. inflata and 7 days for G. ruber). However, this time period is taken from the moment the export of shells starts, not the time of life before that, which may be anywhere from two weeks to a full year. How does a living foram population respond to perturbances like eddies, or do they only generate a pulse of settling shells?"*

The two cyclonic eddies focused on in this study both remained over the sediment trap site from between 1 month (January-February 2009) up to 3 months (April-June 2010). Both of these eddies span a typical PF lifecycle (2-weeks to a month) and would have lasted long enough for the next generation of PF to respond. In this study, the 2009 eddy coincided with this narrow reproductive window of the deeper-dwellers (*globorotaliid* species e.g. *G. truncatulinoides*) and boosted their numbers, through increasing their food availability in addition to aiding their vertical migration through destabilisation of the water column. The large flux of *globorotaliid* species, in particular *G. truncatulinoides*, associated with a cyclonic eddy e.g. in 2009 (this study) and 2007 (unpublished results) suggests that the physical disruption of the water column benefits the reproduction of this particular species. A pulse of settling shells would be less species-specific and presumably represent increased numbers of all PF species abundant at that time rather than just this one.

We suggest that eddies enhance the existing seasonal cycle which is dominantly constrained by MLD and food availability, rather than sparking spontaneous production of foraminifera.

4. *"Fig. 3a. From the graph it seems that the relationship of PF flux to Chla concentration is curvilinear rather than rectilinear, i.e. while Chla increases, PF fluxes level off. If so, linear correlation is not warranted."*

We could amend the trendline in Figure 3a from linear to curvilinear but this produces a smaller r^2 suggesting that the dominant relationship is actually linear. In addition, we have no reason to believe that there should be less sensitivity of PF flux at higher Chl *a* concentrations.

5. *"Given the title of the paper (".. strength of the carbonate pump.."), what is the contribution of planktonic foraminifera to the carbonate mass flux?"*

~40 % of total carbonate flux during winter as stated in the submitted manuscript:

- Abstract, page 12224, line 11
- Section 4.2, page 12231, line 27-28
- Section 6, page 12236, line 29
- Section 7, page 12237, line 18

6. *“Conclusions, 7, line 16-19: The authors argue that the heavy tests of particularly the winter globorotaliids “...may serve as ballasting mechanisms for carbonate...”. It is unclear, however, what is meant here as the large heavy tests concerned have settling velocities that exceed those of organic matter aggregates and would settle as individual particles rather than ballasting these aggregates as e.g. coccoliths do. Please clarify and include the reasoning in the discussion of results rather than in the conclusions.”*

The use of term ‘ballasting’ was used to describe the *Globorotaliid* tests as ballasts for their own carbonate as they are three times denser than surface dwelling species. These tests do not aggregate with other particles but settle out of water column quickly due to their high settling velocities. We are happy to change this as below.

Adding a sentence to Section 5.1.1, Page 12234, line 5. Changes are shown in bold italic:

“We thus conclude that the depth of the mixed layer plays an important role in regulating PF flux by controlling the abundance and timing of their food availability. ***This in turn controls the flux of the denser tests of Globorotaliids (up to three times denser than surface species). These tests accelerate the transfer of carbonate from surface to deep ocean, thereby strengthening the carbonate pump.***

And changing Conclusion, 7, page 12238, line 17 to:

“We suggest that these dense carbonate tests (***up to three times denser than surface dwellers***) may ***strengthen the carbonate pump by accelerating the transfer of carbonate from surface to deep ocean*** and contribute up to 40% of the contemporaneous peak in total carbonate export fluxes”

7. *“There are various repetitive typos with respect to taxonomy that need correction: Globorotalia rather than Globoratalia; crassaformis rather than crassiformis; Globigeri- noides rather than Globignerioides”*

Corrected.

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Upper ocean mixing controls the seasonality of planktonic foraminifer fluxes and associated strength of the carbonate pump in the oligotrophic North Atlantic

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Abstract

Oligotrophic regions represent up to 75% of Earth's open-ocean environments. They are thus areas of major importance in understanding the plankton community dynamics and biogeochemical fluxes. Here we present fluxes of total planktonic foraminifera and eleven planktonic foraminifer species measured at the Oceanic Flux Program (OFP) time series site in the oligotrophic Sargasso Sea, subtropical western North Atlantic Ocean. Foraminifera flux was measured at 1500 m water depth, over two ~2.5 year intervals, 1998-2000 and 2007-2010. We find that foraminifera flux was closely correlated with total mass flux, carbonate and organic carbon fluxes. We show that the planktonic foraminifera flux increases approximately five-fold during the winter-spring, contributing up to ~40% of the total carbonate flux. This was primarily driven by increased fluxes of deeper dwelling globorotaliid species, which contributed up to 90% of the foraminiferal-derived carbonate during late winter-early spring. Interannual variability in total foraminifera flux, and in particular fluxes of the deep dwelling species (*Globorotalia truncatulinoides, Globorotalia hirsuta and Globorotalia inflata*), was related to differences in seasonal mixed layer dynamics affecting the strength of the spring phytoplankton bloom and export flux, and by the

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passage of mesoscale eddies. As these heavily calcified, dense carbonate tests of deeper dwelling species (3 times denser than surface dwellers) have greater sinking rates, this implies a high seasonality of the biological carbonate pump in oligotrophic oceanic regions. Our data suggest that climate cycles, such as the North Atlantic Oscillation, which modulates nutrient supply into the euphotic zone and the strength of the spring bloom, may also in turn modulate the production and flux of these heavily calcified deep-dwelling foraminifera by increasing their food supply, thereby intensifying the biological carbonate pump.

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1. Introduction

Planktonic foraminifera (PF) comprise 23-56% of the total open marine calcite flux and thus exert an important control on global carbon cycling (Schiebel, 2002). They are used extensively in palaeoceanographic and palaeoclimatic reconstructions via utilisation of their species abundance and assemblage composition (e.g., Lutz, 2011; Sexton and Norris, 2011), geochemical signatures (e.g., Zeebe et al. 2008), shell mass (e.g., Barker and Elderfield, 2002) and in evolutionary and biogeographic studies (e.g. Sexton and Norris, 2008). However, gaps remain in our understanding of the controls on their spatial and temporal distribution in the upper water column. Following the early 1980s when sea surface temperatures (SSTs) were thought to dominantly control PF distributions and abundance (CLIMAP project members, 1994), a number of other environmental parameters have also been shown to exert influence on the distribution and abundance of PF, such as salinity (Kuroyanagi and Kawahata, 2004), productivity, nutrient availability (Schiebel, 2002, Northcote et al. 2005, Žarić et al. 2005; Storz et al. 2009; Sexton and Norris, 2011) and water column stability (Hemleben et al. 1989, Lohmann and Schweitzer 1990, King and Howard, 2003). It is thus imperative to better understand the environmental factors controlling modern-day PF abundance in order to produce accurate interpretations of palaeorecords based on PF assemblages.

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The response of PF flux and species composition to environmental and/or oceanographic factors have been studied using plankton tow materials which can give information about living populations' species distribution and depth habitats within the upper ocean (Tolderlund and Be, 1971, Fairbanks et al., 1980; Schiebel 2002). However, temporal resolution is often limited when using plankton tows. The continuous time series records provided by sediment-traps allow a more complete understanding of the seasonal and interannual changes in PF flux and can aid in integrating living assemblages with the sedimentary record.

Earlier studies of planktonic foraminifer flux off Bermuda at the Seasonal Changes in Foraminifera Flux (SCIFF) site (Figure 1) (Deuser et al. 1981, Hemleben et al. 1985, Deuser 1987, Deuser and Ross 1989) were based on a bi-monthly sampling interval and provide a general description of foraminifera flux, species composition and seasonality. These studies found that PF >125µm comprise on average 22% of the total calcium carbonate flux in the Sargasso Sea (Deuser and Ross 1989), although this average underestimates the importance of the PF flux contribution during different seasons. Here we utilise a higher resolution bi-weekly sediment trap time series from the Oceanic Flux Program (OFP), ideal for studying the detailed response of PF species flux to physical oceanographic changes because PF species lifespan is approximately 2-3 weeks (Spero, 1998, Erez et al. 1991). These samples also benefit from the availability of upper ocean hydrographic and biogeochemical data collected at the nearby Bermuda Atlantic Time Series (BATS) site, as well as remote sensing data, which allows us to evaluate the environmental factors that control the total foraminifer flux as well as the response of individual species flux. Furthermore, we assess the relative contribution of PF flux to regional carbonate export and explore the implications of our findings for carbonate cycling in the oligotrophic North Atlantic.

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2. Oceanographic Setting

The Sargasso Sea is located within the North Atlantic gyre, which is characterised by high temperatures and salinities, and weak, variable surface currents (Lomas et al. 2013 and references therein). The OFP and BATS sites are situated in a transition region between the northern eutrophic waters and the relatively oligotrophic subtropical convergence zone in the south (Steinberg et al. 2001 and references therein). Subtropical Mode Water (STMW) forms on the fringes, north of the gyre, owing to convective deep winter mixing and entrainment of nutrients and is characterized by temperatures of 17.8-18.4°C and salinities of ~36.5 +/- 0.05 (Bates et al. 2002), typically occurring between ~250-400 m water depth (Bates, 2007).

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The hydrography and biogeochemistry of the area have been summarized by Michaels and Knap (1996), Steinberg et al. (2001), Lomas et al. (2013) and references therein. In the absence of large changes in salinity, the 10°C seasonal change in surface temperatures driven by solar insolation, controls the shoaling and erosion of the mixed layer, which reaches a maximum of 250-400m in late winter, increasing vertical mixing and entraining nutrient-rich waters. The depth of mixing determines the strength of seasonal particulate flux, nutrient concentrations and primary production during the subsequent spring bloom (Michaels and Knap, 1996, Steinberg et al., 2001). With the onset of seasonal stratification in late February-March, a spring bloom develops when phytoplankton biomass and particulate organic carbon standing stocks are maximal. As seasonal stratification intensifies, a nutrient-depleted, shallow surface mixed layer develops which is underlain by a subsurface chlorophyll maximum at approximately 80-100m depth. Strong stratification in summer and

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autumn results in low vertical mixing that limits nutrient availability and primary production. Seasonal cooling in late autumn results in erosion and gradual deepening of the mixed layer, with renewed nutrient entrainment into the euphotic zone and an increase in primary production. Mesoscale physical variability in this area is the dominant method of nutrient transport (McGillicuddy et al., 1998). In particular, passage of cyclonic and mode water eddies may lead to nutrient entrainment which generates short-lived phytoplankton blooms and community restructuring (Wiebe and Joyce, 1992, Olaizola et al., 1993, McNeil et al., 1999, Letelier et al., 2000, Seki et al., 2001, Sweeny et al., 2003) which could, in turn, impact higher trophic levels such as planktonic foraminifera.   In addition, these blooms often result in short-lived, episodic periods of enhanced export fluxes of labile organic material to depth (Conte et al. 1998, 2003, 2014).

3. Materials and methods

3.1 The OFP Sediment trap time-series

The OFP mooring is located at 31° 50'N, 64° 10'W, about 55 km southeast of Bermuda at 4200m water depth (Figure 1). Three Mark VII Parflux sediment traps (McLane Labs, Falmouth, MA) are deployed at depths of 500 m, 1500 m and 3200 m. The traps (0.5 m^2 surface area) are programmed to collect a continuous bi-weekly time-series of the particle flux. Collected samples were processed according to Conte et al. (2001) and split into < 125 µm, 125-500 µm, 500-1000 µm and >1000 µm size fractions. We analyzed foraminifera in the 125-500 µm and 500-1000 µm size fractions of 1500m trap samples collected during two time periods: 1998-2000 and 2008-2010 (109 samples total). We selected the two equivalent 2.5 year intervals a decade apart to generate a bi-weekly resolved time-series which would enable assessment of seasonality as well as interannual variability. Our analyses focused on eleven species that fall within three general groupings: i) surface dwelling species living within the upper 50 m water column (*Globigerinoides ruber var*. white/pink, *Globigerinella siphonifera*, *Globigerinoides sacculifer*), ii) intermediate dwelling species living in the ~50-200 m depth range (*Orbulina universa*, *Globigerinoides conglobatus*, *Neogloboquadrina dutertrei*, *Pulleniatina obliquiloculata*) and iii) deep dwelling species (or species that are thought to calcify over a large depth range) living in the ~100-800 m depth range (*Globorotalia inflata*, *Globorotalia crassaformis*, *Globorotalia truncatulinoides*, *Globorotalia hirsuta*). Our assignments of the depth habitats were based on measured species depth distributions and/or inferred distributions based on oxygen isotopic composition (Fairbanks et al., 1980, Anand et

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al., 2003). The temporal offset between the foraminiferal species fluxes reaching the trap at 1500m depth versus the timing of these species' growth in overlying waters will vary depending on habitat depths and individual species' sinking rates (Takahashi and Bé, 1984). A surface-dwelling *G. ruber* living at 25 m depth may sink at ~198 m day^{-1}, taking ~7 days to reach the 1500 m trap, whereas a more heavily calcified deeper-dwelling species such as *G. inflata* may sink ~504 m day^{-1}, taking only ~3 days to reach the 1500 m trap. These fast sinking rates are much shorter than the typical lifespans of PF and are thus not anticipated to cause any offset between the hydrographic and sediment trap flux data (Honjo and Manganini, 1993).

On average, ~440 tests were counted in each sample fraction. To generate the flux data, counts of total and individual foraminifera species in the sample aliquots for each size fraction was converted to total counts per sample fraction and then the totals for the two fractions were combined (i.e. total planktonic foraminifera between 125-1000 um in size). Total counts were then scaled for the processing split (60%) and converted to flux (tests m^{-2} d^{-1}).

3.2 BATS and remote sensing data

The BATS site (31^{0}40'N, 64^{0}10'W) is located just south of the OFP mooring (Figure 1). Monthly hydrographic and biogeochemical data collected by the BATS time-series was obtained from the BATS website (http://bats.bios.edu). Mixed layer depth (MLD) was available from Lomas et al. (2013) and was calculated from CTD profiles using the variable sigma-*t* criterion equivalent to a 0.2°C temperature change (Sprintall and Tomczak, 1992). The mesoscale eddy field was assessed using

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interpolated data on sea surface anomaly available from the CCAR Global Historical Gridded SSH Data Viewer (http://eddy.colorado.edu/ccar/ssh/hist_global_grid_viewer).

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4.1. Total planktonic foraminiferal fluxes

4.1.1. In relation to other mass fluxes

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The seasonal cycle and interannual variability of the PF flux at 1500m depth is highly correlated with that of the total mass, carbonate and organic carbon fluxes. All fluxes are strongly characterized by an abrupt spring maximum during February-April, which varies significantly on an interannual basis (Figure 2). For example, the spring PF flux peak ranged from a low of 400 tests m^{-2} day^{-1} in 2008, coinciding with minimal spring mass fluxes, to a high of 900 tests m^{-2} day^{-1} in 2009, coinciding with an extreme peak in spring mass fluxes. All fluxes typically drop to a minimum over the summer months (May-August) and remain low until the following spring bloom. During these minima, the PF flux generally amounts to <200 tests/m^2/day. In some years (e.g. 2009 and, to a lesser extent, 2008), the PF flux displays a smaller, but distinct second peak in the months September-October. This secondary autumn peak can also be seen in the mass flux and carbonate flux in 2009 but is absent in the organic carbon flux. Over the entire record, the correlation between PF flux and mass, carbonate and organic carbon flux is 0.65, 0.64 and 0.55, respectively.

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4.1.2 Relative to upper ocean hydrography

In Figure 3 we compare interannual variations in bi-weekly resolved total PF flux to ~monthly resolved changes in key upper ocean hydrographic parameters, measured at the BATS site. PF flux exhibits an inverse relationship with seasonal variations in sea surface temperatures (SST) and reaches a maximum when SST is coolest in January-

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March (Figure 3a). Of note, is the particularly large and prolonged PF bloom in 2010, which coincided with a cyclonic eddy that passed through the area causing the lowest SSTs on record for this site ~18.9°C (Figure 3a-b). Sea level anomaly (SLA) provides information about eddies passing through the area (Figure 3b). A negative anomaly is associated with cyclonic eddies and a positive anomaly associated with anticyclonic and mode water eddies. The SLA data show that the particularly high and prolonged PF fluxes, total mass flux and organic carbon flux in spring 2009 and 2010 coincided with the passage of cold, cyclonic eddies (Figure 2), which enhance nutrient upwelling into the euphotic zone.

The annual and interannual PF flux is in phase with the deepening and shoaling of the mixed layer depth (MLD) (Figure 3c) and with chlorophyll *a* concentrations (Figure 3d). The seasonal PF flux maximum coincides with the chlorophyll *a* maximum (which is used here as a proxy for the spring phytoplankton bloom) and the organic carbon flux from 200m, which represents organic carbon export from surface productivity (Figure 3e), and the deepest MLD during February-March. During April-May, the MLD shoals back towards the surface coinciding with decreasing chlorophyll *a* concentrations and PF flux. The strong correlations between the seasonality in PF flux and that of primary production and export is demonstrated by the regressions between total PF flux and chlorophyll *a* concentration (Figure. 4a) and the 1500m mass flux (Figure. 4b). During the winter-spring period the magnitude of PF flux generally follows the evolution in MLD and is maximal when the MLD is maximal (Figure. 4c). However, when the mixed layer depth shoals to <80 m during the low productivity period in late spring and summer, this correlation is not significant (Figure. 4d).

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4.2 Planktonic foraminifera species fluxes

In general, all planktonic foraminifera, and especially deeper dwelling species, show strong, consistent seasonal variance (Figures 5-7). Our results demonstrate a clear depth progression towards more pronounced seasonality in the deeper species, compared to a larger intra-seasonal variability in the surface and intermediate dwellers. In addition, the deep dwelling PF species exhibit repeatable species successions throughout the winter and early spring (Figure 8, Table 1). Figure 8 shows that *Globorotalia truncatulinoides* dominates the flux of deeper dwellers, and thrives each December, reaching a maximum during January. *G. truncatulinoides* is then followed by *G. hirsuta*, *G. crassaformis*, and *G. inflata* which all peak between March and April. *G. truncatulinoides* displays large interannual variability (Table 1), ranging from lows of ~4000 tests/m^2/year in 2009-2010 to highs of up to ~14 000 tests/m^2/year in 1999-2000 (Figure 6). The remaining deeper dwellers (*Globorotalia hirsuta*, *Globorotalia inflata*, *Globorotalia crassaformis*) also vary on an interannual basis. Figure 7 and Table 1 show that the largest fluxes of deeper dwelling species occurred during the winter/spring of 1999-2000 and 2008-2009. Using shell weights from this study averaged with shell weights (125-1000um) measured by Deuser, (1987) and Deuser and Ross, (1989), we estimate that PF flux contributes up to ~40% of the total carbonate flux during winter-spring but <10% during summer (Figure 9a). Deeper dwelling species account for 60-90% of PF carbonate flux (Figure 9b) and up to 37.5% of the total carbonate flux (e.g. during the winter-spring of 2000) (Figure 9c).

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5. Discussion

The controls on PF flux in the Sargasso Sea was first introduced by Bé, (1960) and later developed by Tolderlund and Bé, (1971) who suggested that PF flux is dominantly controlled by the availability of their food phytoplankton. Thus, the environmental factors controlling PF flux should be closely aligned with the factors controlling phytoplankton productivity and export flux.

5.1 Environmental controls on PF fluxes

5.1.1. Depth of the mixed layer

Previous studies suggest that increased chlorophyll concentrations and larger phytoplankton abundances occur when the MLD deepens (Townsend et al. 1994, Waniek, 2003, Nelson et al. 2004) and the amplitude and timing of MLD deepening determines the size of the following spring bloom (Menzel and Ryther, 1961, Michaels et al. 1994). Here, we also observe a simultaneous seasonal peak in chlorophyll *a* and maximum depth of the MLD, as observed by previous studies at BATS (Steinberg et al. 2001, Cianca et al. 2012), the timing and amplitude of which coincides with the maximum PF flux (Figure. 3c, d). Similarly, seasonal changes in mixed layer depth are closely associated with changes in foraminifer production (Thunell and Reynolds, 1984, Sautter and Thunell, 1989, Pujol and Vergnaud Grazzini 1995, Schmuker and Sciebel 2002) and chlorophyll *a* concentrations (King and Howard, 2003, 2005) in other ocean basins. Siegel et al. (2002) proposed that south of 40°N, the initiation and extent of the spring bloom is dominantly limited by

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nutrients, and this is supported by the simultaneous increase in phytoplankton concentrations with mixing depth at BATS (Treusch et al. 2012). Vertical mixing in late winter and spring distributes nutrients into the euphotic zone to support the spring phytoplankton bloom, causing the consequent seasonal peak in export fluxes of organic carbon, to fuel symbiont-barren foraminifera production (Figure. 2d). In contrast, no correlation exists between PF flux and MLD during the late spring to autumn when the mixed layer fails to penetrate the minimum depth of the deep chlorophyll maximum layer (~80m), where many species of planktonic foraminifera reside in association with other zooplankton and algal cells (Fairbanks and Wiebe, 1980) (Figure 4d). This is also the depth of the nitricline where nitrate concentrations > 0.1 umol kg^{-1}, (Sciebel et al. 2001).

The majority of the increased PF flux in the winter-spring is driven by increased fluxes of deeper dwelling species, in particular *G. truncatulinoides* and *G. hirsuta* (Figure. 9b). These species are symbiont-barren and rely on the flux of phytodetritus and other labile organic carbon as a food source from the spring phytoplankton bloom (Hemleben et al. 1989). The discrepancy in timing of peaks between the deeper dwelling species (Figure 8) is likely due to subtle changes in phytoplankton succession related to the species' diets (Deuser and Ross, 1989, Hemleben et al. 1989). Overall, the seasonal PF species succession is broadly similar to previous observations from 1959-63 and 1978-84 (Tolderlund and Bé, 1971, Deuser 1987, Deuser and Ross, 1989) which suggests that despite long-term environmental change, species seasonality have remained consistent over the past 50 years.

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The correlation observed here between the seasonality in the PF flux, chlorophyll *a* concentration and mass flux at 1500m (Figure 4 a and b) clearly demonstrates that the seasonality of non symbiont-bearing foraminifera, such as the globorotaliids is, controlled by phytoplankton production and the export flux of phytodetritus to depth. As these globorotaliids are up to three times denser than surface species (unpublished data), their sinking rates are significantly higher than those of other species. Thus, increased production by these species can accelerate the transfer of carbonate from surface to deep-ocean, thereby strengthening the carbonate pump.

In contrast, the surface-dwelling symbiont-bearing foraminifera have lifecycles which strongly benefit from stratified surface waters and shallow mixed layers in order to photosynthesise allowing them to succeed in low nutrient conditions (Hemleben et al. 1989). Surface dwellers generally calcify in late summer when sea surface temperatures are at a maximum and dinoflagellates are abundant (Tolderlund and Bé, 1971). We thus conclude that the depth and structure of the mixed layer plays an important role in regulating PF species flux by controlling the abundance and timing of their food availability throughout the seasonal cycle.

5.1.2. MLD deepening and shoaling rates

Current models based on the light-limited higher latitudes (Waniek, 2003; Mao, Y., 2013- personal communication), suggest that if the MLD shoals early and slowly, the consequent bloom will be long and weak compared to if the MLD shoals late and quickly, which causes a short and sharp bloom. At our subtropical study site, the spring bloom is predominantly limited by nutrient input into the euphotic zone, which

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is determined by the depth of the mixed layer. Increased heat loss and wind stress leading to higher convective mixing during the winter months controls the rate of deepening of the mixed layer, which is strongly correlated to the maximum MLD reached ($r^2 = 0.88$) (Figure 10a). Years with faster deepening rates have deeper mixed layers and hence larger spring blooms (e.g. winter 2009), whereas slow deepening rates cause shallower mixed layers and smaller spring blooms. There is also some evidence that light-limitation could be a secondary control on the peak productivity of the spring bloom at this site (Dutkiewicz et al. 2001, Lomas et al. 2009, Cianca et al. 2012) as the euphotic zone extends to ~100m (Steinberg et al. 2001) and a faster shoaling rate during the spring could control could concentrate the food available for symbiotic-foraminifera in the euphotic zone, resulting in a larger PF flux.

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To test whether the rates of mixed layer deepening in early winter and of shoaling in spring affect the PF flux, we computed a mixed layer dynamics index, D_r/S_r, which is the ratio of the rate of deepening to the rate of shoaling and compared this to the integrated PF flux (Table 2). The D_r/S_r ratio never exceeds 1, indicating that the shoaling rate always exceeds the deepening rate. For all the years studied, there is a strong inverse relationship between the integrated PF flux over the duration of spring bloom, and the D_r/S_r ratio (Figure 10b, $r^2 = 0.93$). This relationship is also present in the maximum in chlorophyll *a* concentration and the D_r/S_r ratio (Figure 10c, $r^2 = 0.76$). This correlation indicates that when the MLD shoals more quickly during spring stratification (lower D_r/S_r ratio), the chlorophyll *a* concentrations and PF flux are higher, as supported by a strong correlation ($r^2 = 0.87$) between shoaling rate and integrated PF flux (Figure 10d).

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Years where the shoaling rate is twice as quick as the deepening rate (e.g. winters 1997, 2008, and 2009) have average D_r/S_r ratios, average-length blooms and PF flux (~30 tests/m^2/day, Table 2). Years with comparatively equal rates of shoaling and deepening (e.g. winter 2007) have larger D_r/S_r ratios, longer and slower blooms with shallower MLDs and small PF fluxes. Years when the shoaling rate is much quicker than deepening rate e.g. winter 1999 have the smallest D_r/S_r ratios and shorter, sharper blooms with greater numbers of intermediate thermocline dwelling species such as *N. dutertrei*, *P. oblquiloculata*, *G. siphonifera*, suggesting that when the rate of shoaling is higher the seasonal thermocline is nearer to the surface for longer, which is beneficial for these symbiont-bearing and symbiont-facultative species. The PF fluxes were large (and prolonged) respectively in winter 2008-09 and 2009-10 despite having average D_r/S_r ratios but were probably enhanced by additional factors discussed in the next section.

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5.1.3 Eddies

The negative sea level anomalies in spring of 2009 and 2010 indicate that the large (and in 2010 prolonged) PF fluxes in these years were clearly associated with the passage of cyclonic eddies (Figure 3b). Eddy pumping of nitrate into the euphotic zone has been shown to significantly increase new production (Oschlies and Garçon, 1998, Oschlies, 2002). Cianca et al. (2007) estimate that eddy pumping contributes ~50% of the nutrient input into the euphotic zone in the Sargasso Sea. Studies at the BATS site have demonstrated the influence of cyclonic and mode water eddies in promoting phytoplankton blooms and increased secondary production (Eden et al., 2009, McGillicuddy et al. 2007, Goldthwait and Steinberg, 2008, McGillicuddy et al., 1999, Sweeney et al., 2003, Lomas et al. 2013, Cianca et al. 2012) and therefore affecting PF food availability and quality (Schmuker and Schiebel, 2002). Previous studies have found higher fluxes of certain PF species such as *Globigerinita glutinata* associated with cyclonic eddy structures in the Caribbean Sea (Schmuker and Schiebel, 2002) and North Atlantic (Beckman et al. 1987), also in conjunction with upwelling frontal regions in the Mexican Pacific (Machain-Castillo et al. 2008) and deep mixed layers during winter in the Mediterranean (Pujol and Vergnaud Grazzini, 1995). Here we observe a similar response during the passage of a cyclonic eddy in spring 2009, particularly for deeper dwelling species. In fact, the largest PF flux observed over the entire record was associated with this eddy passage, even though the maximum MLD and D_r/S_r were modest (Table 2). Similarly, the mass and organic carbon flux measured during passage of this eddy (Figure. 2b-d) were the highest fluxes measured over the last 25 years of the OFP time-series, indicating that the conditions in this eddy promoted an extremely large export flux to fuel the production

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of deep dwelling foraminifera species such as *G. truncatulinoides*, *G. hirsuta*, and especially *G. inflata* which all experienced higher seasonal fluxes in 2009 (Figure 7).

This observation is consistent with an exceptionally large increase in the flux of *G. truncatulinoides* (> 600 tests m^{-2} day^{-1}) seen at the OFP traps during the spring of 2007, which was also influenced by the passage of a productive cyclonic eddy (Fang et al. 2010, Conte et al. 2014). Both the 2007 and 2009 eddies occurred between January-March during the seasonal flux of the deeper dwellers (Figure 7), underscoring the importance of the timing of eddy passage in enhancing PF flux. The influence of eddies here is similar to observations from the Eastern Mediterranean where increased numbers of grazing species such as *G. truncatulinoides* and *G. inflata*, have been found in association with eddy structures and deep mixed layers (Pujol and Vergnaud Grazzini, 1995). These findings suggest that productive cyclonic eddies, when co-occurring with deep MLDs, act to enhance the existing seasonal abundance of deeper dwelling species through mixing of the water column, which aids their annual reproductive migration in addition to increasing food supply.

Along with the timing of the eddy passage, our observations also suggest that the PF flux response is dependent on whether the eddy is intensifying or weakening. For instance, both cyclonic eddies in 2009 and 2010 intensified over the spring bloom (Figure 3b) eliciting a large biological response indicated by elevated subsurface Chl-*a* concentrations and increased PF flux. In contrast, the cyclonic eddy in winter 2007-08 was weakening over the spring bloom and therefore elicited no PF flux response. Recent studies have found that eddies which are a minimum of 1-2 months in duration are more likely to induce a larger biological response (Mouriño-Carballido and

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McGillicuddy, 2006, Sweeny et al. 2003). Our observations also suggest that eddies need to be present for at least a month to elicit responses in the flux of PF which have minimum lifecycles of two weeks. For instance, in winter 1998-99 a cyclonic eddy passed over the sediment trap site in only one month and elicited no biological response, compared to cyclonic eddies in 2009 and 2010, which both remained over the site for a minimum of 2-3 months and elicited large biological responses (Figure 3b). These findings suggest that cyclonic eddies which intensify over the spring bloom and last for 1-3 months can elicit a significant biological response and increased PF flux.

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6. Implications

Our results show that environmental factors and mesoscale eddy variability play an important role in regulating the planktonic foraminifera fluxes, by regulating the MLD and consequent magnitude of the spring bloom and biological export flux.

An overarching climatological variable affecting this region especially is the North Atlantic Oscillation (NAO), which exerts a strong influence on air temperature, storminess, heat loss, winter mixed layer depth, and, therefore, nutrient injection into the upper ocean during the winter months (Bates, 2012 Bates and Hansell, 2004, Rodwell et al. 1999). Modelling studies have shown that when the NAO is in its low phase, i.e. negative NAO (e.g. winter 2010), there is increased heat loss that intensifies convective mixing and results in enhanced nutrient upwelling into the euphotic zone to support primary production (Oschlies, 2001). The NAO influence on upper ocean productivity and biogeochemical fluxes is demonstrated by the inverse correlation between the wintertime (NDJF) NAO index and the deep particulate nitrogen flux in the OFP traps over a thirty-year period (Conte and Weber, 2014) and increased primary productivity in negative wintertime NAO phases (Lomas et al. 2010). If convective mixing and nutrient entrainment into the euphotic zone is stronger during negative NAO years, this could serve to modulate PF flux, and therefore carbonate flux, on decadal timescales. When we compare PF fluxes covering a range of NAO indexes, from this study using the 1500m trap to the 3200m trap between 1978-84 (Deuser and Ross, 1989, Deuser, 1987), we find a weak inverse correlation between total PF flux and (DJFM) NAO index in-phase (not significant), but we do find a significant inverse correlation with a (DJFM) NAO with a 1-year lag

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($p < 0.005$) (Figure 11). Cianca et al. (2012) showed that their correlation between winter NAO and total Chlorophyll *a* at BATS improved when applying a +1 year time lag, but still remained insignificant. They attributed this to variability in the subtropical mode water, which can laterally advect nutrients on interannual timescales (Palter et al. 2005, Patara et al. 2011). We acknowledge that additional longer-term data is needed to test the mechanism behind this correlation, but our results suggest that changes in NAO status and/or mesoscale eddy frequency could significantly modulate planktonic foraminifera flux and export flux from the surface ocean on interannual timescales.

This study shows that the productivity of the dominant deep dwelling species *G. truncatulinoides* and *G. hirsuta* is especially responsive to interannual variability in overlying surface water conditions and especially to the transient high production/flux events that are associated with the passage of productive cyclonic eddies that coincide with their seasonal spring production peak. Our data show that deeper dwelling species can account for up to ~90% of the total PF carbonate flux, representing up to ~40% of the total carbonate flux during winter-spring at the OFP site. Changes in NAO status, which modulates nutrient supply into the euphotic zone and the strength of the spring bloom, also may in turn modulate the production and flux of these heavily calcified deep-dwelling foraminifera by increasing their food supply, thereby intensifying the carbonate pump.

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7.0. Conclusions

Our study demonstrates that the interannual variability in planktonic foraminifera flux can be linked to the MLD and the rate of deepening/shoaling of the mixed layer associated with nutrient injection into the euphotic zone. We find that higher PF fluxes coincide with deeper MLDs, especially when combined with cyclonic eddy-induced nutrient upwelling. In particular, the production of the dominant deep dwelling species *G. truncatulinoides* and *G. hirsuta* is shown to be particularly responsive to interannual variability in overlying surface water conditions and especially to the transient high production/flux events that are associated with productive cyclonic eddies. These species dominate the major late winter-early spring pulses of foraminifera and have higher sinking rates than surface dwelling species because they are up to three times denser (unpublished results). We suggest deeper-dwelling species strengthen the carbonate pump by accelerating the transfer of carbonate from surface to deep ocean and contribute up to 40% of the contemporaneous peak in total carbonate export fluxes. It follows that any increase in fluxes of these deep-dwellers arising from climate-induced changes in winter-spring mixed layer dynamics will also increase the average sinking rate of foraminiferal carbonate and intensify the overall carbonate pump. Our findings suggest that the North Atlantic Oscillation, via its influence on mixed layer depth, nutrient upwelling, phytoplankton production and export flux may also serve to modulate the foraminiferal component of the carbonate pump in the subtropical North Atlantic.

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Acknowledgements

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Figure Captions

Figure 1. Map to show locations of the Oceanic Flux Program (OFP) mooring (31°50'N, 64°10'W) and the Bermuda Atlantic Time Series (BATS) hydrographic station (31°50'N, 64°10'W) and Seasonal Changes in Foraminifera Flux (SCIFF) site and Hydrostation S in relation to Bermuda Island.

Figure 2. Temporal changes in total planktonic foraminifera flux and mass, carbonate, and organic carbon fluxes at 1500 m depth over the six year study period.

Figure 3. Temporal changes in environmental parameters measured at the BATS site in relation to total planktic foraminiferal flux in the 1500m OFP trap (thin, black line) a) Sea surface temperature (0-25 m), b) Sea level height anomaly; grey bars indicate periods when productive cyclonic eddies influenced the site, c) Mixed layer depth, d) Chlorophyll *a* concentration (0-25 m average) e) Average organic carbon flux at 200 m

Figure 4. Correlation between total planktonic foraminifera flux in the 1500 m OFP trap (thin, black line) with environmental parameters measured at the BATS site. a) Chlorophyll *a* concentration at 0-25 m. The correlation excludes an anomalous peak in chlorophyll *a* concentration observed in 2010. b) MLDs >80 m, excluding the extremely deep MLD observed in 2010. c) MLDs <80 m.

Figure 5. Temporal changes in surface dwelling planktic foraminifera fluxes in the 1500m trap with changes in sea surface temperature (0-25 m) shown in the dashed

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black line for reference. The approximate depth habitat (Anand et al. 2003) is shown on figures.

Figure 6. Temporal changes in intermediate dwelling planktonic foraminifera fluxes in the 1500 m trap with changes in sea surface temperature (0-25 m) for reference. The approximate depth habitat (Anand et al. 2003) is shown on figures.

Figure 7. Temporal changes in deeper dwelling planktonic foraminifera fluxes in the 1500 m trap with changes in sea surface temperature (0-25 m) for reference. The approximate depth habitat (Anand et al. 2003) is shown on figures. Graphs are ordered according to seasonal succession.

Figure 8. Seasonal succession for deeper dwelling species averaged over six spring blooms (1998, 1999, 2000, 2008, 2009, 2010) from the 1500 m trap. *G. truncatulinoides, G. hirsuta, G. inflata* appear on the left axis and *G. crassaformis* is on the right axis.

Figure 9. a) The relative contribution of total PF to total carbonate flux b) The relative contribution of deeper dwelling planktonic foraminifera (*G. hirsuta, G. truncatulinoides, G. crassaformis, G. inflata)* to the total planktonic foraminiferal carbonate flux c) The relative contribution of total deeper dwellers (*G. hirsuta, G. truncatulinoides, G. crassaformis, G. inflata*) to the total carbonate flux. All graphs show four full years 1998-99, 1999-00, 2008-09 and 2009-10.

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Figure 10. a) Correlation between the maximum mixed layer depth and deepening rate of the mixed layer for years 1995-2011. Correlation between the deepening:sholaing rate (D_r/S_r) ratio of the mixed layer depth for all years studies excluding 2000 and b) Integrated PF flux during the spring blooms which ranged from Dec-May c) maximum chlorophyll *a* concentrations in the surface ocean during the spring bloom for all years studied, excluding the anomalous year 2010 in parentheses d) Correlation between the shoaling rate and integrated flux of total PF over the spring bloom period which ranged from Dec-May. Diamonds indicate years with eddy influence 2009 and diamond with parentheses = 2010. Round points are years without eddy influence.

Figure 11. Annual integrated PF flux from this study (1500m trap, square symbols) and 1979-1984 (*3200m trap, round symbols, Deuser, 1987, Deuser and Ross, 1989) plotted against wintertime (DJFM) NAO index + 1 year lag. Annual fluxes from both trap depths are comparable. **Annual PF flux from 1978 (diamond symbol) was not included in the regression because it was an anomalously low flux year which could be explained by a shallow MLD and/or possibly the presence of an anticyclonic eddy (no data to test), which may have suppressed the spring bloom and hence PF flux as seen during 1994 at BATS (Lomas et al. 2013). NAO data available from http://www.cpc.ncep.noaa.gov/data/teledoc/nao.shtml

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Table 1. Annual fluxes for planktonic foraminifera species at 1500 m depth in 1998-1999, 1999-2000, 2008-2009 and 2009-2010 and the four-year averages. Fluxes were calculated from the sum of biweekly averages between July-June for each year and converted to tests m^{-2} yr^{-1}. Species are listed according to their estimated depth habitats.

		Annual flux (tests m^{-2} yr^{-1})					
Species	Seasonal flux maximum	1998-1999	1999-2000	2008-2009	2009-2010	Average	3200m avg (1978-1984)[3]
Surface dwellers:							
G. ruber (pink)	July-Sept	2524	1978	1576	2122	2050	1450
G. ruber (white)	Sept-Oct	16 197	19 633	13 917	18 719	17 117	
G. sacculifer	Oct[1]. March[2]	256	292	1007	348	1903	425
Surface Totals		18 977	21 903	16 500	21 189	17 346	
Intermediate dwellers:							
G. siphonifera	*	6101	3182	2231	2833	3587	
O. universa	April-May[1], Oct-Nov[2]	1429	694	1056	2250	1357	
G. conglobatus	Nov	277	180	0	4	115	300
N. dutertrei	March-April[1], Nov-Dec[2]	1290	185	471	839	696	876
P. obliquiloculata	Dec-March	398	205	708	352	416	762
Intermediate Totals		9495	4446	4466	6278	6171	
Deep dwellers:							
G. truncatulinoides	Jan-Feb	5248	13 796	9517	4031	8148	3420
G. hirsuta	Feb-March	1784	9888	3859	2770	4575	1520
G. crassaformis	Feb-March	26	100	122	139	97	192
G. inflata	March-April	844	995	1652	1869	1340	1270
Deep Totals		7902	24 779	15 150	8809	14 160	5402
Other species	-	51 442	43 704	43 172	70 446	51 191	
Totals	-	87 816	94 831	79 289	106 722	92 165	

[1] Primary peak

[2] Secondary peak

[3] Averages from Deuser and Ross, 1989

* This species has low seasonality

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Table 2. Mixed layer depth and mean rates of mixed layer (ML) deepening and shoaling. The D_r/S_r ratio is a derived value calculated from the rate of ML deepening divided by the rate of ML shoaling (see text). The winter-spring PF flux represents the PF flux integrated over the whole bloom, which varied interannually in length but ranged from Dec-May. Shaded years indicate years when a cyclonic eddy was present during the spring bloom period.

Year	MLD max (m)	ML Deepening Rate (m day^{-1})	ML Shoaling Rate (m day^{-1})	D_r/S_r ratio (m)	Maximum PF flux (tests m^{-2} day^{-1})	Integrated winter-spring PF flux (tests m^{-2} day^{-1})
1997-1998	235	0.93	1.91	0.49	641	28
1998-1999	222	0.78	7.78	0.10	816	41
1999-2000	197	0.63	Data missing	-	761	30
2007-2008	130	0.55	0.75	0.73	385	17
2008-2009	198	0.95	2.21	0.43	946	28
2009-2010	464	1.76	3.82	0.46	815	32

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