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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, and are typically characterized by nutrient-limited upper-ocean mixed layers. 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 from a bi-weekly sediment trap time series in the oligotrophic Sargasso Sea, subtropical western North Atlantic Ocean at 1500 m water depth, over two ~ 2.5 year intervals, 1998–2000 and 2007–2010. Foraminifera flux was closely correlated with total mass flux and with 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, driven primarily by increased fluxes of deeper dwelling (“globorotaliid”) species. Interannual variability in total foraminifera flux, and in particular fluxes of the deep dwelling *Globorotalia truncatulinoides*, *Globorotalia hirsuta*, *Globorotalia inflata*, were related to differences in seasonal mixed layer dynamics affecting the strength of the spring phytoplankton bloom and export flux, and by the passage of mesoscale eddies. The heavily calcified, dense carbonate tests of deeper dwelling species (3 times denser than surface dwellers) can contribute up to 90 % of the foraminiferal-derived carbonate in this region during late winter-early spring, implying a high seasonality of the biological carbonate pump in oligotrophic oceanic regions. Our data suggest that climate cycles, such as the North Atlantic Oscillation, that modulate the depth of the mixed layer, intensity of nutrient upwelling and primary production could also modulate the strength of the biological carbonate pump in the oligotrophic North Atlantic.

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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; Žaric et al., 2005; Storz et al., 2009; Sexton and Norris, 2011) and water column stability (Hemleben et al., 1989; Lohmann and Schweitzer, 1990). In addition, different environmental variables may induce species-specific responses (Kuroyanagi and Kawahata, 2004). 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.

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.

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Previous work has shown that PF > 125 μm comprise on average 22 % of the total calcium carbonate flux in the Sargasso Sea (Deuser and Ross, 1989), but this underestimates the importance of their contribution which may vary on a seasonal scale. Initial studies of planktonic foraminifer flux in the Oceanic Flux Program (OFP) sediment traps off Bermuda (Deuser et al., 1981; Hemleben et al., 1985; Deuser, 1987; Deuser and Ross, 1989) were based on a bi-monthly trap cup sampling interval and provided a general description of foraminifera flux, species composition and seasonality. Here we utilise a higher resolution bi-weekly sediment trap time series, covering the 2–3 week lifespan of most PF (Spero, 1998; Erez et al., 1991) that will capture the detailed seasonal response of PF species flux to physical oceanographic changes. These samples also benefit from the availability of upper ocean hydrographic and biogeochemical data collected at the nearby Bermuda Atlantic Time Series (BATS) site, which was not established when the OFP time-series began, 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.

2 Oceanographic setting

The Sargasso Sea is located within the North Atlantic gyre, which is characterised by warm temperatures, high salinities and weak and 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 $\sim 36.5 \pm 0.05$ (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 250–400 m 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 90–100 m depth. Strong stratification in summer and 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; Sweeney 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 4200 m water depth. Three Mark VII Parflux sediment traps (McLane Labs, Fal-

5 mouth, MA) are deployed at depths of 500, 1500 and 3200 m. The traps (0.5 m² 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 and 500–1000 μm size fractions. We analyzed foraminifera in the 125–500 μm and 500–1000 μm size fractions of 1500 m trap samples collected dur-

10 ing two time periods: 1998–2000 and 2007–2010 (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) sur-

15 face dwelling species living within the upper 50 m water column (*Globignerioides ruber* var. white/pink, *Globigerinella siphonifera*, *Globigerinoides sacculifer*), (ii) intermediate dwelling species living in the ~50–200 m depth range (*Orbulina universa*, *Globigneri-*

20 *noides 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 crassiformis*, *Globorotalia truncatulinoides*, *Globorotalia hirsuta*). Our assignments of the depth habi-

tats were based on measured species depth distributions and/or inferred distributions based on isotopic composition (Fairbanks et al., 1980; Anand et al., 2003).

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

25 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 μm in size). Total counts were then scaled for the processing split (60 %) and converted to flux (tests m⁻² d⁻¹).

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3.2 BATS and remote sensing data

The BATS site (31°40' N, 64°10' W) is located just south of the OFP mooring. 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 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). The temporal offset between the foraminiferal species fluxes measured in the 1500 m trap and their growth environment in overlying waters will vary depending on habitat depths and individual 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 calcified deeper-dwelling species such as *G. inflata* may sink ~504 m day⁻¹, taking ~3 days to reach the 1500 m trap. These fast sinking rates are not anticipated to cause any offset between the hydrographic and sediment trap data.

4 Results

4.1 Total planktonic foraminiferal fluxes

4.1.1 Relative to other mass fluxes

The seasonal cycle and interannual variability of the PF flux at 1500 m depth is highly correlated with that of the particle flux and other mass fluxes. All fluxes are strongly characterized by an abrupt spring maximum during February–April, which varies significantly on an interannual basis (Fig. 1). For example, the spring PF flux peak ranged from a low of 400 tests m⁻² d⁻¹ in 2008, coinciding with minimal deep spring fluxes, to

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a high of $900 \text{ tests m}^{-2} \text{ d}^{-1}$ in 2009, coinciding with an extreme peak in deep spring 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 $< 200 \text{ tests m}^{-2} \text{ d}^{-1}$. 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.

4.1.2 Relative to upper ocean hydrography

In Fig. 2 we compare interannual variations in bi-weekly resolved total PF flux to \sim 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–March (Fig. 2a). Of note, is the particularly large and prolonged PF bloom in 2010, which coincides with the coldest SSTs on record for this site $\sim 18.9^\circ\text{C}$.

Sea level anomaly (SLA) provides information about eddies passing through the area (Fig. 2b). 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 fluxes in PF, total mass flux and organic carbon (Fig. 1) in spring 2009 and 2010 coincided with the passage of cyclonic eddies, 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) (Fig. 2c) and with chlorophyll *a* concentrations (Fig. 2d). 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 200 m, which represents organic carbon export from surface productivity (Fig. 2e),

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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 (Fig. 3a) and the 1500 m mass flux (Fig. 3b). During the winter–spring period the magnitude of PF flux generally follows the evolution in MLD and is maximal when the MLD is maximal (Fig. 3c). However, when the mixed layer depth shoals to < 80 m during the low productivity period in late spring and summer, this correlation breaks down (Fig. 3d).

4.2 Planktonic foraminifera species fluxes

In general, all planktonic foraminifera, and especially deeper dwelling species, show strong, consistent seasonal variance (Figs. 4–6). 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 (Fig. 7). Figure 7 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* and *G. crassiformis*, both reaching their maxima in March, closely followed by *G. inflata*, which peaks between March and April. *G. truncatulinoides* displays large interannual variability (Table 1), ranging from lows of ~ 4000 tests $\text{m}^{-2} \text{yr}^{-1}$ in 2009–2010 to highs of up to $\sim 14\,000$ tests $\text{m}^{-2} \text{yr}^{-1}$ in 1999–2000 (Fig. 6). The remaining deeper dwellers (*Globorotalia hirsuta*, *Globorotalia inflata*, *Globorotalia crassiformis*) also vary on an interannual basis. Figure 6 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 (125–1000 μm) measured by Deuser (1987) and Deuser and Ross (1989), we estimate that PF flux contributes up to $\sim 40\%$ of the total carbonate flux during winter–spring but $< 10\%$ during summer (Fig. 8a). Deeper

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dwelling species account for 60–90 % of PF carbonate flux (Fig. 8b) and up to 37.5 % of the total carbonate flux (e.g. during the winter–spring of 2000) (Fig. 8c).

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, the timing and amplitude of which coincides with the maximum PF flux (Fig. 2c and d). Vertical mixing in late winter and spring distribute nutrients into the euphotic zone to support the spring phytoplankton bloom, and in turn the seasonal peak in export fluxes of organic carbon (Fig. 1d) to fuel foraminifera production. In contrast, there is no correlation during the late spring to autumn when the MLD is less than ~ 80 m (Fig. 3d). During this period, the mixed layer fails to penetrate the nitricline (defined at nitrate concentrations $> 0.1 \mu\text{mol kg}^{-1}$, Schiebel et al., 2001).

The majority of the increased PF flux in the winter–spring is driven by an larger fluxes of deeper dwelling species, in particular *G. truncatulinoides* and *G. hirsuta* (Fig. 8b), which are symbiont-barren and rely on the flux of phytodetritus and other labile organic

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carbon as a food source from the spring phytoplankton bloom (Hemleben et al., 1989). The correlation observed here between the in the PF flux, chlorophyll *a* concentration (Fig. 3a) and the 1500 m mass flux (Fig. 3b) clearly demonstrates that the seasonality of non symbiont-bearing foraminifera is strongly controlled by phytoplankton production and the export flux of phytodetritus to depth. 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.

5.1.2 MLD deepening and shoaling rates

Current models based on the light-limited higher latitudes (Waniek, 2003; Y. Mao, personal communication, 2013), 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 mean rate of deepening of the mixed layer between October and January is strongly correlated to the maximum MLD reached ($r^2 = 0.88$) (Fig. 9a). If the MLD maximum is deeper, then the consequent shoaling rate in spring is also more likely to be higher.

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 PF flux maximum (Table 2). The D_r/S_r ratio never exceeds 1, indicating that the shoaling rate always exceeds the deepening rate and variability of the shoaling rate mainly controls changes in the D_r/S_r ratio. For all the years studied, there is a strong inverse relationship between the average PF flux over the duration of spring bloom, and the D_r/S_r ratio (Fig. 9b, $r^2 = 0.93$). This is also mirrored in the maximum in chlorophyll *a* concentration and the D_r/S_r ratio (Fig. 9c, $r^2 = 0.76$). This correlation suggests 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 ($r^2 = 0.93$) between shoaling rate and PF flux over the duration of the bloom (Fig. 9d). For example, an unusually fast shoaling rate and deep MLD in 1999 led

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to a large but short maximum in PF flux, whereas the large PF flux in spring 2010 coincided with an exceptionally deep MLD. As the winter–spring PF flux maximum is largely associated with increased fluxes of deeper dwelling species, this relationship further implies greater export fluxes to depth during periods of more rapid MLD shoaling to fuel deep foraminifera production and thereby strengthen the seasonal carbonate pump. Conversely, the slow deepening rate in the winter of 2007 yielded an especially shallow MLD in 2008 and the subsequently slow shoaling rate in spring 2008 produced the smallest spring peak in PF flux of all the years studied (Table 2). Both the large (and prolonged) PF fluxes in spring 2009 and 2010 respectively were probably enhanced by additional factors discussed in the next section.

5.2 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 (Fig. 2b). Eddies contribute ~30–73% nitrate required by new production into the euphotic zone in the Sargasso Sea, promoting phytoplankton blooms (Eden et al., 2009; Goldthwait and Steinberg, 2008; McGillicuddy et al., 1998, 1999, 2007; Sweeney et al., 2003; McGillicuddy and Robinson, 1997) and therefore food for PF and increasing PF flux. Although the maximum MLD in 2009 was modest and the average rates of mixed layer deepening and shoaling were similar to lower flux years, the spring 2009 peak in PF flux was the largest flux observed over the entire record, (Table 2). The chlorophyll *a* concentrations measured at BATS during the 2009 eddy were not elevated, but the mass and organic carbon flux measured during passage of this eddy (Fig. 1b–d) were the highest fluxes measured over the last 25 years of the OFP time-series. This indicates that the conditions in this eddy promoted an extremely large carbon export flux to fuel the production of non-symbiont bearing foraminifera species such as *G. truncatulinoides*, *G. hirsuta*, and especially *G. inflata* which all experienced higher seasonal fluxes in 2009 (Fig. 6). This observation is consistent with an exceptionally large increase in the flux of *G. truncatulinoides*

($> 600 \text{ tests m}^{-2} \text{ d}^{-1}$) seen at the OFP traps during the spring of 2007, which similarly was influenced by the passage of a productive cyclonic eddy (Fang et al., 2010). Both the 2007 and 2009 eddies occurred between January–March during the seasonal flux of the deeper dwellers (Fig. 6). The seasonal abundance of deeper dwellers seem to be enhanced by the passage of the cyclonic eddies, which may aid their annual reproductive migration through mixing of the water column, in addition to driving a large carbon export flux.

Occurrence of cyclonic eddies synchronous with deep MLDs during the winter can enhance the overall PF flux by increasing cyclonic mixing and chlorophyll concentrations. For instance, 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 large cyclonic eddy and a particularly negative NAO index. The combination of a negative NAO with a cyclonic eddy caused a dramatic increase in chlorophyll *a* concentrations (Fig. 2d), prolonging the PF flux and all other mass fluxes (Fig. 1).

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 (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 biogeochemi-

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cal 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). If convective mixing and nutrient entrainment into the euphotic zone is stronger during negative NAO years such as 2010 (e.g. Fig. 2c), this could serve to modulate PF flux, and therefore carbonate flux, on decadal timescales. To test this, we compare PF fluxes in NAO negative years (e.g. 2009–2010 – this study) to total PF fluxes averaged from the NAO positive/neutral years (e.g. 1982–1983 – from Deuser, 1987; Deuser and Ross, 1989), and 1998–1999 – this study. As a first order comparison, the average PF flux during the NAO positive/neutral years of 1982–1983 and 1998–1999 are $\sim 90\,000\text{ tests m}^{-2}\text{ yr}^{-1}$ (or an average of $247\text{ tests m}^{-2}\text{ d}^{-1}$) whereas total PF fluxes for the NAO negative year of 2009–2010 was notably higher at $\sim 107\,000\text{ tests m}^{-2}\text{ yr}^{-1}$ ($292\text{ tests m}^{-2}\text{ d}^{-1}$). The PF flux in the NAO negative year (2009–2010) is thus $\sim 19\%$ higher than the average across the NAO positive/neutral years (1982–1983 and 1998–1999). This finding provides support for our hypothesis that a negative NAO index (perhaps via amplified cyclonic eddy activity) stimulates a substantial increase in not only total PF flux, but also in mass flux, carbonate flux and organic carbon flux, which were respectively $\sim 38\%$, $\sim 39\%$, and $\sim 31\%$ higher in 2009–2010 (negative NAO), compared to 1998–1999 (positive NAO) (no data for 1982–1983). We recognize that further study is needed to ascertain how much of this PF flux response is due to negative-NAO strengthened winter-time mixing or cyclonic eddy activity, but our results suggest that changes in NAO status and/or mesoscale eddy frequency could significantly modulate total particulate flux, planktonic foraminifera flux and export flux from the surface ocean.

In particular, the production of the dominant deep dwelling species *G. truncatulinoides* and *G. hirsuta* are especially 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 that coincide with their seasonal production. Our estimations show that deeper dwelling species can account for up to $\sim 90\%$ of the total PF carbonate flux, representing up to $\sim 40\%$ of the total carbonate

flux during winter–spring at the OFP site. It therefore follows that changes in NAO status and/or mesoscale eddy frequency are likely to significantly modulate the total flux of these heavily calcified deep-dwelling foraminifera, thereby intensifying the carbonate pump.

7 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 as they contain more carbonate per test (Deuser et al., 1981). We suggest that these dense carbonate tests may serve as ballasting mechanisms for carbonate as they are up to three times denser (unpublished results) and contribute up to 40 % of the contemporaneous peak in total carbonate export fluxes. It follows therefore that any increased fluxes of deep-dwellers due to 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 and nutrient upwelling, may also modulate the total planktonic foraminiferal flux and the foraminiferal component of the carbonate pump in the subtropical North Atlantic on decadal timescales.

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Table 1. Annual fluxes for planktic foraminiferal 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 $\text{m}^{-2} \text{yr}^{-1}$. Species are listed according to their estimated depth habitats.

Species	Seasonal flux maximum	Annual flux (tests $\text{m}^{-2} \text{yr}^{-1}$)				Average	3200 m avg (1978–1984) ³
		1998–1999	1999–2000	2008–2009	2009–2010		
Surface dwellers:							
<i>G. ruber</i> (pink)	Jul–Sep	2524	1978	1576	2122	2050	1450
<i>G. ruber</i> (white)	Sep–Oct	16 197	19 633	13 917	18 719	17 117	
<i>G. sacculifer</i>	Oct ¹ , Mar ²	256	292	1007	348	1903	425
Surface Totals		18 977	21 903	16 500	21 189	17 346	
Intermediate dwellers:							
<i>G. siphonifera</i>	⁴	6101	3182	2231	2833	3587	
<i>O. universa</i>	Apr–May ¹ , Oct–Nov ²	1429	694	1056	2250	1357	
<i>G. conglobatus</i>	Nov	277	180	0	4	115	300
<i>N. dutertrei</i>	Mar–Apr ¹ , Nov–Dec ²	1290	185	471	839	696	876
<i>P. obliquiloculata</i>	Dec–Mar	398	205	708	352	416	762
Intermediate Totals		9495	4446	4466	6278	6171	
Deep dwellers:							
<i>G. truncatulinoides</i>	Jan–Feb	5248	13 796	9517	4031	8148	3420
<i>G. hirsuta</i>	Feb–Mar	1784	9888	3859	2770	4575	1520
<i>G. crassiformis</i>	Feb–Mar	26	100	122	139	97	192
<i>G. inflata</i>	Mar–Apr	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).

⁴ 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 average PF flux over the whole bloom, which ranged from December–May. Bold faced years indicate years when a cyclonic eddy was present during the spring bloom period.

Year	MLD max (m)	ML Deepening Rate (m d^{-1})	ML Shoaling Rate (m d^{-1})	D_r/S_r ratio (m)	Maximum PF flux ($\text{tests m}^{-2} \text{d}^{-1}$)	Average winter–spring PF flux ($\text{tests m}^{-2} \text{d}^{-1}$)
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	1.71	0.37	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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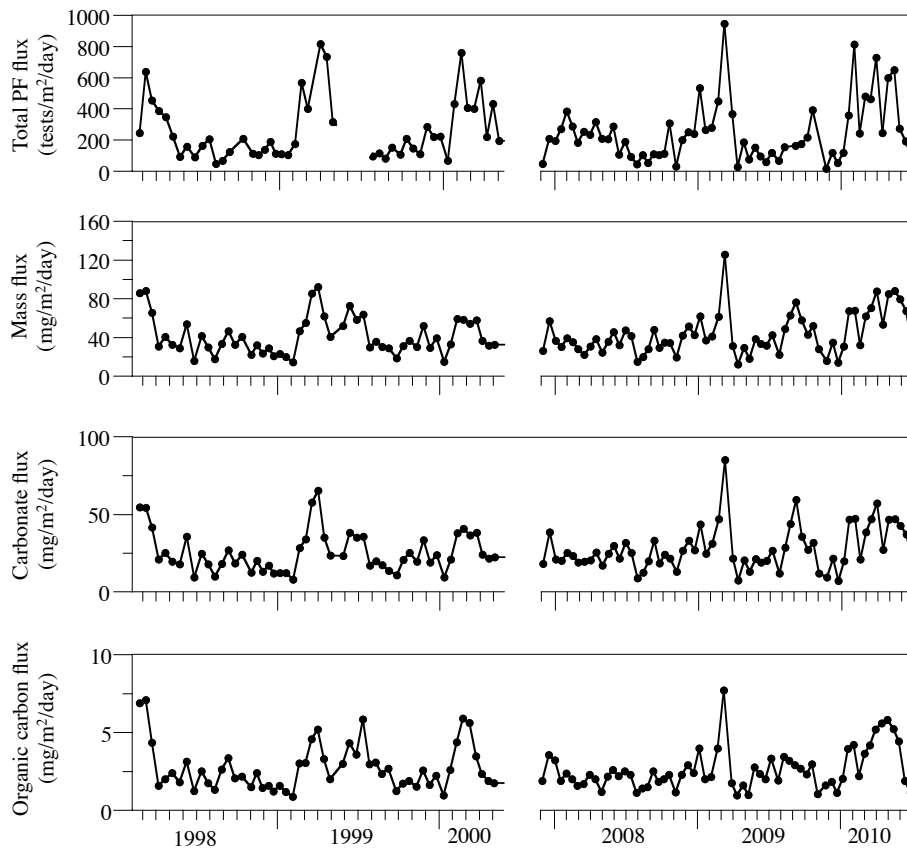


Figure 1. Temporal changes in total planktic foraminiferal flux and mass, carbonate, and organic carbon fluxes at 1500 m depth over the six year study period.

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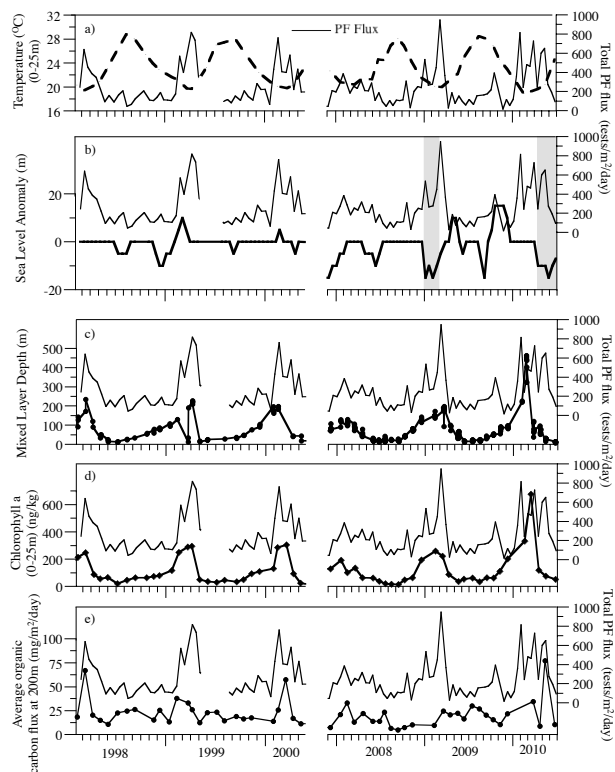


Figure 2. Temporal changes in environmental parameters measured at the BATS site in relation to total planktic foraminifer flux in the 1500 m OFP trap (thin, black line). **(a)** Sea surface temperature (0–25 m), **(b)** sea level height anomaly; grey bars indicate periods when productive cyclonic eddies influenced the site, **(c)** mixed layer depth, **(d)** chlorophyll a concentration (0–25 m average), **(e)** average organic carbon flux at 200 m.

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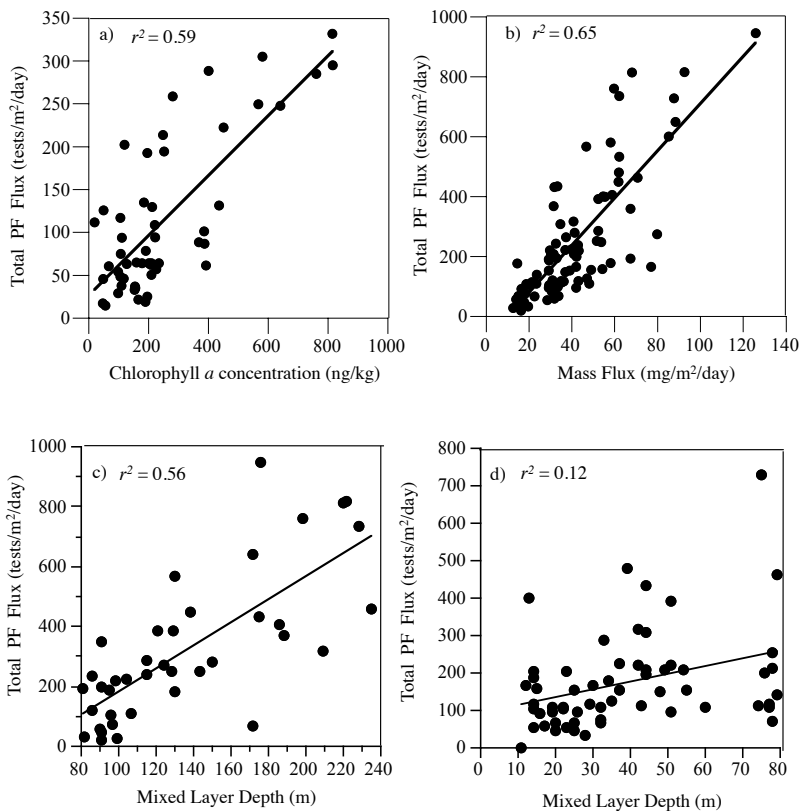


Figure 3. Correlation between total planktonic foraminiferal flux and mass flux in the 1500 m OFP trap with environmental parameters measured at the BATS site **(a)** Chlorophyll *a* concentration at 0–25 m. The correlation excludes an anomalous peak in chlorophyll *a* concentration observed in 2010. **(b)** Regression with mass flux **(c)** MLDs > 80 m, excluding the extremely deep MLD observed in 2010. **(d)** MLDs < 80 m.

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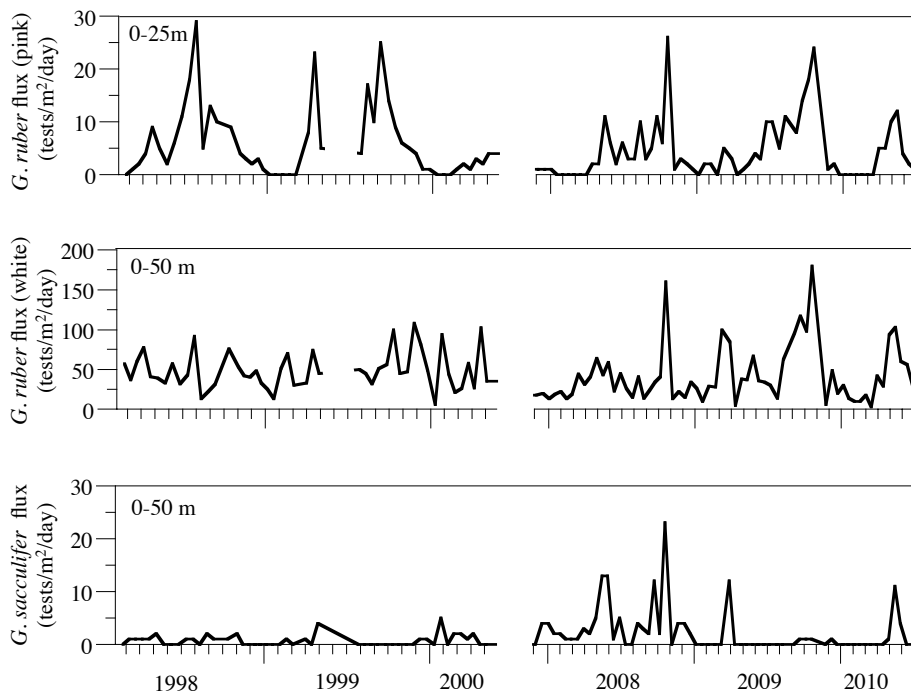


Figure 4. Temporal changes in surface dwelling planktic foraminifera fluxes in the 1500 m trap. The approximate depth habitat (Anand et al., 2003) is shown on figures.

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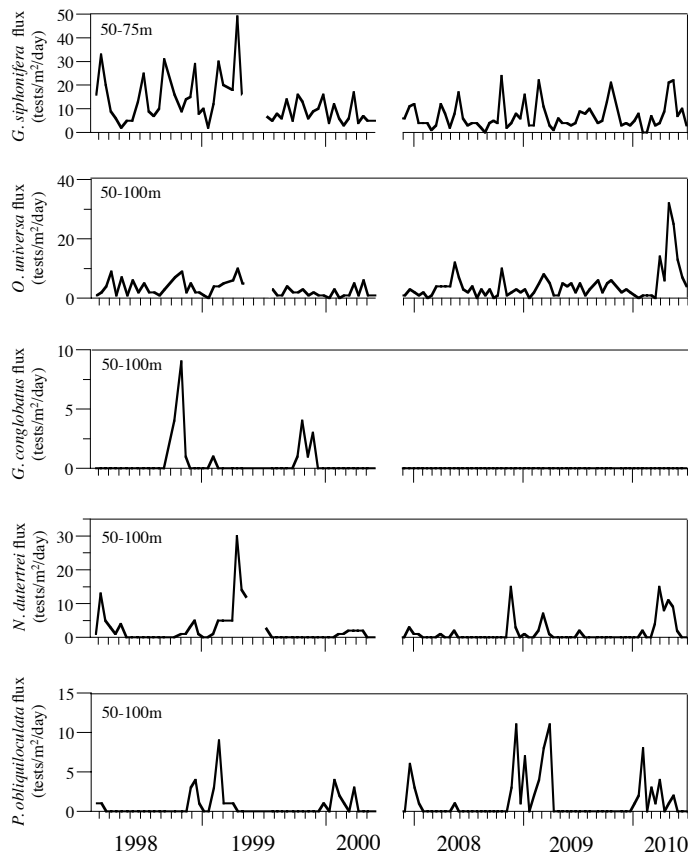


Figure 5. Temporal changes in intermediate dwelling planktic foraminifera fluxes in the 1500 m trap. The approximate depth habitat (Anand et al., 2003) is shown on figures.

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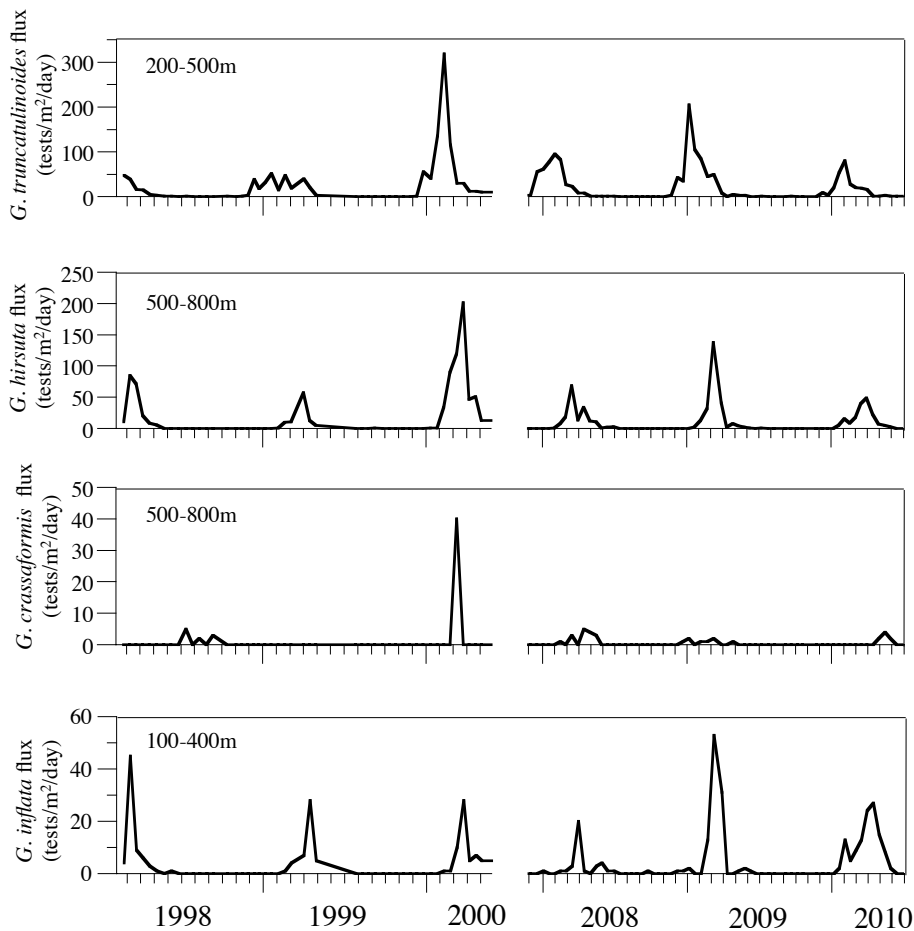


Figure 6. Temporal changes in deeper dwelling planktic foraminifera fluxes in the 1500 m trap. The approximate depth habitat (Anand et al., 2003) is shown on figures. Graphs are ordered according to seasonal succession.

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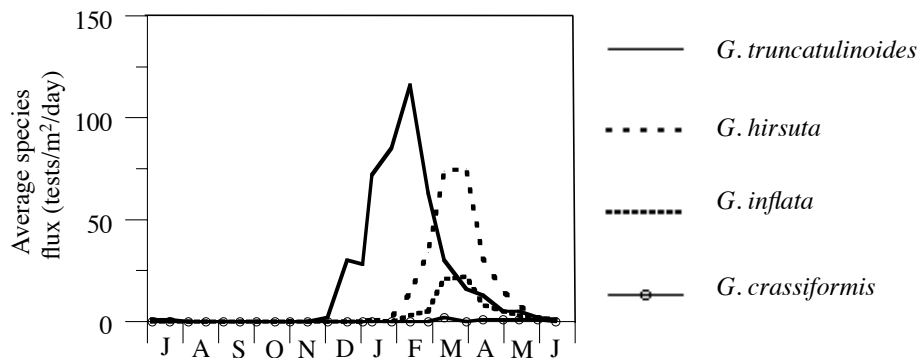


Figure 7. Seasonal succession for deeper dwelling species averaged over six spring blooms (1998, 1999, 2000, 2008, 2009, 2010), *G. truncatulinoides*, *G. hirsuta*, *G. inflata* and *G. crassiformis* from the 1500 m trap.

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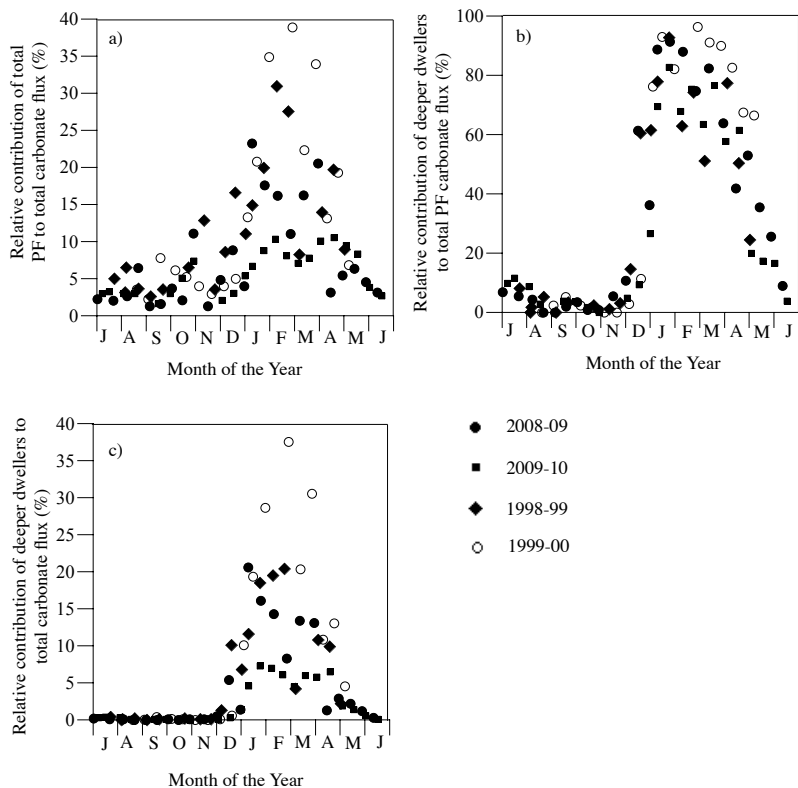


Figure 8. (a) The relative contribution of total PF to total carbonate flux. (b) The relative contribution of deeper dwelling planktonic foraminifera (*G. hirsuta*, *G. truncatulinoides*, *G. crassiformis*, *G. inflata*) to the total planktonic foraminiferal carbonate flux. (c) The relative contribution of total deeper dwellers (*G. hirsuta*, *G. truncatulinoides*, *G. crassiformis*, *G. inflata*) to the total carbonate flux. All graphs show four full years 1998–1999, 1999–2000, 2008–2009 and 2009–2010.

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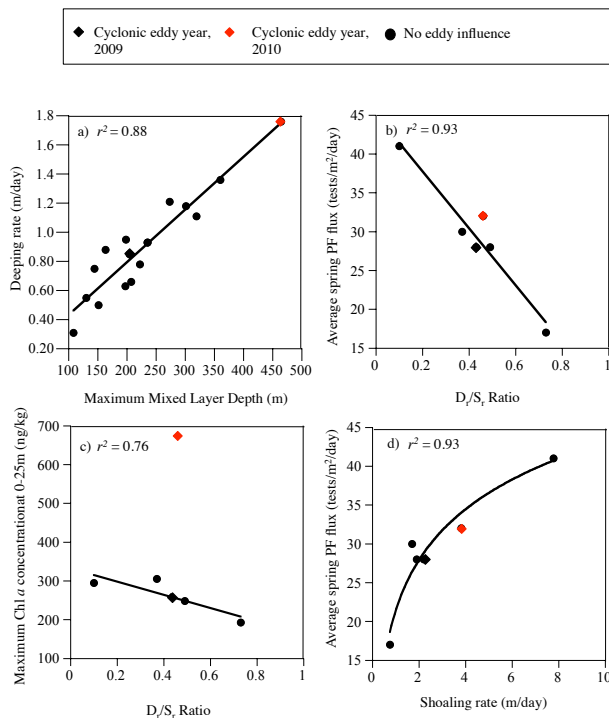


Figure 9. (a) Correlation between the maximum mixed layer depth and deepening rate of the mixed layer for years 1995–2011. Correlation between the deepening : shoaling rate (D_r/S_r) ratio of the mixed layer depth and (b) average PF flux during the spring blooms for all years studied (December–May) (c) maximum chlorophyll *a* concentrations in the surface ocean during the spring bloom for all years studied. (d) Correlation between the shoaling rate and average flux of total PF over the spring bloom period (December–May). Diamonds indicate years with eddy influence, where the black = 2009 and the red = 2010. Round points are years without eddy influence.