

# 1 Global analysis of seasonality in the shell flux of extant 2 planktonic foraminifera

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## 10 11 Abstract

12 Shell fluxes of planktonic foraminifera species vary intra-annually in a pattern that appears to  
13 follow the seasonal cycle. However, the variation in the timing and prominence of seasonal  
14 flux maxima in space and among species remain poorly constrained. Thus, although  
15 changing seasonality may result in a flux-weighted temperature offset of more than 5°C  
16 within a species, this effect is often ignored in the interpretation of foraminifera-based  
17 paleoceanographic records. Here we present an analysis of the intra-annual pattern of shell  
18 flux variability in 37 globally distributed time series. The existence of a seasonal component  
19 in flux variability was objectively characterised using periodic regression. This analysis  
20 yielded estimates of the number, timing and prominence of seasonal flux maxima. Over 80%  
21 of the flux series across all species showed a statistically significant periodic component,  
22 indicating that a considerable part of the intra-annual flux variability is predictable.

23 Temperature appears to be a powerful predictor of flux seasonality, but its effect differs  
24 among species. Three different modes of seasonality are distinguishable. Tropical and  
25 subtropical species (*G. ruber* (white and pink varieties), *N. dutertrei*, *G. sacculifer*, *O.*  
26 *universa*, *G. siphonifera*, *P. obliquiloculata*, *G. menardii*, *G. rubescens*, *G. tenella* and *G.*  
27 *conglobatus*) appear to have a less predictable flux pattern with random peak timing in warm  
28 waters. In colder waters, seasonality is more prevalent: peak fluxes occur shortly after  
29 summer temperature maxima and peak prominence increases. This tendency is stronger in  
30 species with a narrower temperature range, implying that warm-adapted species find it

1 increasingly difficult to reproduce outside their optimum temperature range and that with  
2 decreasing mean temperature, their flux is progressively focussed into the warm season. The  
3 second group includes the temperate to cold-water species *Globigerina bulloides*, *G.*  
4 *glutinata*, *N. incompta*, *N. pachyderma*, *G. scitula*, *G. calida*, *G. falconensis*, *G. theyeri* and  
5 *G. uvula*. These species show a highly predictable seasonal pattern with one to two peaks a  
6 year, which occur earlier in warmer waters. Peak prominence in this group is independent of  
7 temperature. The earlier-when-warmer pattern in this group is related to the timing of  
8 productivity maxima. Finally, the deep dwelling *G. truncatulinoides* and *G. inflata* show a  
9 regular and pronounced peak in winter/spring. The remarkably low flux outside the main  
10 pulse may indicate a long reproductive cycle of these species. Overall, our analysis indicates  
11 that the seasonality of planktonic foraminifera shell flux is predictable and reveals the  
12 existence of distinct modes of phenology among species. We evaluate the effect of changing  
13 seasonality on paleoceanographic reconstructions and find that, irrespective of the seasonality  
14 mode, the actual magnitude of environmental change will be underestimated. The observed  
15 constraints on flux seasonality can serve as the basis for predictive modelling of flux pattern.  
16 As long as the diversity of species seasonality is accounted for in such models, the results can  
17 be used to improve reconstructions of the magnitude of environmental change in  
18 paleoceanographic records.

19

## 20 **1. Introduction**

21 Planktonic foraminifera are unicellular marine zooplankton with a global distribution. About  
22 40 morphospecies are known as extant and a number of these are symbiont-bearing  
23 (Hemleben et al., 1989). Planktonic foraminifera build a calcite shell, which rapidly sinks  
24 after the death of the organism (Takahashi and Bé, 1984). Above the carbonate compensation  
25 depth these shells are well preserved and may form an important part of the sediment. As a  
26 result, planktonic foraminifera play a significant role in the marine carbonate cycle (Schiebel,  
27 2002) and their fossil record is an important source of information on the physical and  
28 chemical conditions of past oceans. However, the interpretation of foraminifera-based proxies  
29 of past environmental change is not straightforward and requires detailed knowledge on the  
30 ecology of the species involved.

31

1 The abundance of planktonic foraminifera and the export flux of their shells vary both  
2 spatially and temporally (e.g. Bé, 1960; Bé and Tolderlund, 1971; Deuser et al., 1981). Time  
3 scales of temporal variability range from less than a month (lunar), to seasonal, inter-annual  
4 and beyond (e.g. Deuser et al., 1981; Marchant et al., 2004; Spindler et al., 1979). The intra-  
5 annual variability can range over several orders of magnitude (Deuser et al., 1981; Tolderlund  
6 and Bé, 1971) and because it resonates with the seasonal cycle of environmental conditions it  
7 has a particularly large potential to modify the proxy signal recorded in a fossil assemblage.  
8 For example, apart from in the tropics, the seasonal sea surface temperature variability is  
9 always greater than the interannual variability (Mackas et al., 2012). Hence, a thorough  
10 understanding of the seasonal cycle in planktonic foraminifera is essential to improve our  
11 ability to reconstruct past ocean changes.

12

13 Like in other groups of marine plankton, seasonality in planktonic foraminifera can in  
14 principle manifest itself in two ways: i) through changes in the timing of the peak flux or peak  
15 abundance and ii) through changes in the amplitude of the seasonal cycle. Both aspects of  
16 seasonality could affect planktonic foraminifera proxies, leading to seasonal biases in the  
17 variables recorded by fossil assemblages. In case of temperature reconstructions this can lead  
18 to offsets from mean conditions by several degrees (e.g. Fraile et al., 2009a; Jonkers et al.,  
19 2010). Differences in the seasonal pattern of shell flux among species have been exploited to  
20 reconstruct variations in seasonal temperatures (Saher et al., 2007). In addition, seasonality is  
21 thought to explain part of the difference between foraminifera-based and other proxies  
22 (Laepple and Huybers, 2013; Leduc et al., 2010).

23

24 Besides being species specific (Deuser et al., 1981), seasonality in planktonic foraminifera  
25 fluxes also varies spatially within individual species (Tolderlund and Bé, 1971), implying that  
26 the seasonal cycle is under environmental control. Consequently, seasonality may have  
27 changed as a function of climate and/or oceanic change through time. Until now, few studies  
28 have investigated the effect of such transient changes in seasonality on foraminiferal records.  
29 Using a foraminifera model coupled to global simulations with an ecosystem model Fraile et  
30 al. (2009b) have shown that the timing of maximum production of foraminifera species could  
31 have shifted by as much as six months between the last glacial maximum and the present day,

1 but explicit efforts to quantify seasonal bias in planktonic foraminiferal proxies remain  
2 challenging (Schneider et al., 2010).

3  
4 In most sediment trap studies, the recurrence time of the flux peaks is linked to the seasonal  
5 pattern of temperature (Zaric et al., 2005). Clearly, as in other zooplankton (Mackas et al.,  
6 2012; Richardson, 2008), temperature appears to be an important factor controlling phenology  
7 of planktonic foraminifera. However, several other parameters, some(times) correlated with  
8 temperature, such as food availability, nutrient availability, predation, competition, light  
9 availability and salinity have also been suggested to control the phenology of planktonic  
10 foraminifera, particularly within the optimum temperature range of a species (Hemleben et  
11 al., 1989; Northcote and Neil, 2005; Ortiz and Mix, 1992; Ortiz et al., 1995). Until now there  
12 has been no effort to assess flux seasonality in sediment trap records on a global scale. Instead  
13 of an evaluation of observational data, recent investigations of seasonality in planktonic  
14 foraminifera were based on models (Fraile et al., 2008; Lombard et al., 2011; Zaric et al.,  
15 2006). Despite the different approaches, these models provided a reasonable first order  
16 description of the seasonality in planktonic foraminifera. However, our incomplete  
17 understanding of the mechanisms that control seasonality hampers further improvements and  
18 validation of these models and prevents accounting for seasonality effects on paleorecords.  
19 This is in part due to the lack of a global overview of foraminiferal seasonality.

20  
21 Here we present such a synthesis based on a large number of sediment trap time series from  
22 across the world oceans. Sediment traps provide continuous time-series of settling shell  
23 fluxes, typically at a resolution of less than one month and are therefore ideal to study  
24 phenology. Importantly, shell fluxes represent the settling of dead foraminifera and are  
25 strictly speaking not directly related to the abundance of foraminifera in the water column.  
26 Yet only a limited number of repeated plankton net surveys, which are needed to assess  
27 seasonal water column abundance, exist (Field, 2004; Schiebel et al., 1997) and these are  
28 often of too low resolution and duration to assess seasonality. We therefore assess phenology  
29 from the settling fluxes, which are, given the short life span of foraminifera (Hemleben et al.,  
30 1989), likely to be strongly linked to abundance. Our aim is to determine the extent of the  
31 seasonal component in the flux data and evaluate its predictability.

## 2. Data and methods

To analyse seasonality of planktonic foraminifera shell flux, we produced a compilation of globally distributed moored sediment trap time series with a duration of at least one year. Traps close to the sea floor or in the vicinity of (steep) topography that showed influence of resuspended material (for instance the presence of benthic foraminifera) were not considered. In cases where multiple sediment traps were deployed at different depths on the same mooring, we report data from the shallowest trap as this (likely) reduces the catchment area of the trap and the data hence reflect local conditions more closely. The complete data set contains 37 time series (table 1). The sites are unevenly distributed globally with the majority (28) from the northern hemisphere and an important cluster of 8 traps in the northwest Pacific (Fig. 1). Nevertheless, the data span a temperature range of almost 30 °C without large gaps. Trap depths varied between 250 and 5000 m (table 1) and several sites are close to the continents, but only a single sediment trap was deployed at a location with a water depth <1 km. We therefore consider the sites to reflect pelagic settings. The average duration of the time series is 2.75 years and the longer ones are predominantly from the northern hemisphere (Fig. 1). The mean length of the collection interval was 19 days, but varied between 4 days and 1 month (Fig. 2A). Collection intervals were often also variable during the deployments. Most studies reported fluxes of shells >125 or >150 µm; four used narrower size ranges (table 1). We report here on 23 species for which counts in five or more time series are available (table 2). The taxonomy in all time series has been harmonised such that the *Neogloboquadrina pachyderma* (right-coiling) is considered as a separate species and referred to as *N. incompta*, *Globigerinella aequilateralis* is referred to as *G. siphonifera* and *Globigerinoides trilobus* and *G. quadrilobatus* are included in *G. sacculifer*. In addition *G. umbilicata* is considered synonymous with *G. bulloides*. Since very few studies reported coiling direction in *Globorotalia truncatulinoides*, no distinction was made between left and right coiling varieties of this species. Additional remarks specific to individual time series are included in table 1.

To link the observed shell flux patterns to environmental conditions, temperature and productivity data were extracted for the positions of all traps. Temperature has been considered because it is known to play a key role in the phenology of other zooplankton (Mackas et al., 2012; Richardson, 2008). Most of the other parameters suggested to influence

1 phenology of planktonic foraminifera, such as light, mixed layer depth and nutrient  
2 availability only affect their seasonality indirectly by affecting the phytoplankton, a major  
3 food source for many planktonic foraminiferal species. This results in a predictable phase  
4 relationship with zooplankton always lagging phytoplankton. Thus, the inclusion of  
5 temperature and productivity should allow us to study both end-member scenarios with  
6 foraminifera responding exclusively to temperature or following productivity. Because  
7 continuous observations of near surface conditions from the moorings are not available,  
8 temperature data for the upper water column (0-50 m) were taken from the 2009 World Ocean  
9 Atlas (Locarnini et al., 2010). Using climatology data also allows us to use upper ocean  
10 temperatures that are more representative of foraminifera habitat than surface temperatures  
11 derived from remote sensing. Moreover, inter-annual temperature variability at individual  
12 sites is typically small (often less than 1 °C) compared to the temperature differences between  
13 sites (~30 °C) warranting the use of climatology data since our objective is to compare the  
14 patterns among sites. We use sea surface chlorophyll-a concentration data as an indicator of  
15 upper ocean productivity. Since a large part of the shell flux time series predates the era of  
16 satellite observations we use SeaWiFS monthly climatology (data downloaded from  
17 <http://oceancolor.gsfc.nasa.gov/>). This means that inter-annual productivity variability is  
18 ignored, but similar to temperature, the inter-annual range in peak productivity timing at an  
19 individual site (~ one month) is small compared the total range (12 months) considered here.

20

21 To objectively characterise the pattern of the seasonal shell flux we have used periodic  
22 regression, a simple method that is suited for cyclic data at low and variable resolution,  
23 irregular starting point and short duration (Batchelet, 1981; deBruyn and Meeuwig, 2001;  
24 Mackas et al., 2012). Next to an objective test for the presence of systematic time-related  
25 irregularity in flux, it can detect the number of peaks (assuming these occur at harmonics of  
26 the yearly cycle) and describes objectively the magnitude of the peak flux. The method has  
27 been used extensively to describe cyclic phenomena in biology (Bell et al., 2001; deBruyn  
28 and Meeuwig, 2001; Drolet and Barbeau, 2009). Figure 3 illustrates the approach using an  
29 example of *T. quinqueloba* from the Irminger Sea.

30

31 Prior to analysis, zero fluxes were replaced with half of the observed minimum flux and the  
32 data were converted to a log<sub>10</sub> scale. All observations were put on the same time scale by

1 converting the middate of the collection intervals to yeardays, which were subsequently  
2 angular-transformed using  $DOY/365.25 \times 2\pi$ . No attempt was made to correct for settling  
3 time and/or delay due to production.

4 Using linear multiple regression we tested for the presence of one or two cycles in the shell  
5 flux per year by fitting two different models to the observations:

$$6 \quad J(t) = A + B \sin(t) + C \cos(t) \quad \text{Eq. 1}$$

7 and

$$8 \quad J(t) = A + D \sin(2t) + E \cos(2t) \quad \text{Eq. 2}$$

9 where  $J(t)$  is the shell flux at time  $t$ , and A-E are the parameters to be estimated. This  
10 approach yields a robust estimate of the mean – the periodic mean, parameter A in the  
11 equations above - as well as the amplitude and phase angle/peak timing of the shell flux.  
12 Significance of the models was evaluated using ANOVA for multiple regression. Only model  
13 fits that pass this test with 95 % confidence were considered and if both one and two cycle  
14 models were significant, then the model that explained more variance (highest adjusted  $r^2$ )  
15 was chosen. Implicit to this approach are two important assumptions: i) the seasonal shell flux  
16 follows a sinusoidal (i.e. symmetric) pattern and ii) in the case of a model with two cycles per  
17 year, a  $365.25/2$  days spacing between the two peaks. Both assumptions are reasonable given  
18 the ecology of foraminifera and the nature of the data, but to confirm the appropriateness of  
19 the method we have evaluated how well peak timing is estimated.

20

21 To ensure comparison of the estimates of peak timing, dates from sites in the southern  
22 hemisphere were transformed to northern hemisphere equivalents by adding/subtracting 182.5  
23 days. For a similar reason, comparison of flux amplitude was facilitated by normalising the  
24 log-transformed amplitude of peak flux to the periodic mean:

$$25 \quad PP = \log\left(\frac{10^{amplitude}}{10^{per.mean}}\right) \quad \text{Eq. 3}$$

26

27 Expressed in this way, a peak prominence (PP) of 1 describes a situation where the peak flux  
28 is 10 times larger than the annual mean flux, whereas a value of -1 describes a time series  
29 where the flux during the maximum is only elevated by 10% above the annual mean. All  
30 calculations were carried out using R (R core team, 2013) and maps were generated using  
31 package *mapplots* (Gerritsen, 2012).

### 1 **3. Results**

2 The 37 globally distributed time series reveal the presence of large variability in the  
3 partitioning of shell flux to seasons (Fig. S1). The large variation in seasonality among  
4 species, but importantly also within the same species at different locations is evident.  
5 Considerable differences exist between sites close together, but some coherent patterns  
6 appear. Trends towards a peak later in the year/more in summer at higher latitudes are visible  
7 in some species (e.g. *G. bulloides*, *N. incompta*). Interestingly, seasonally varying fluxes do  
8 not appear to be exclusive to the extratropics.

#### 9 **3.1 Evaluating periodic regression**

10 The time series in the database have different and often varying resolution and duration. In  
11 addition, many time series have gaps due to failing sediment trap rotation or unsuccessful  
12 deployments. These factors render objective characterisation of the seasonal cycle challenging  
13 and we therefore apply the method of periodic regression. Given the assumptions underlying  
14 the periodic regression approach we first evaluate the appropriateness of the method to  
15 describe the seasonal shell flux cycles. To this end, we test how well peak timing is estimated  
16 using three species from the longest time series available (Gulf of Lions, site 11, table 1). This  
17 time series is 10 years long and the observed inter-annual variability in the peak timing  
18 (expressed as the mid-point date of the sampling interval with highest flux) for the three  
19 species is 15 to 38 days. This is comparable to the average difference between observed peak  
20 time and the peak time estimated by periodic regression for each year separately (21 to 36  
21 days). The difference between the observed and modelled timing of peak flux reflects aliasing  
22 due to the resolution of the discrete sampling and the assumption of the periodic regression of  
23 a sinusoidal shape of the flux pattern. The fact that the observed inter-annual variability in  
24 peak timing is similar to the precision of the periodic regression puts important constraints on  
25 the method, implying that inter-annual variability in the peak timing (within approximately  
26 one month) cannot be resolved.

27

28 Considering the average resolution of the trap series being 19 days, an inter-annual variability  
29 in peak timing of the same type as observed in the Gulf of Lions series could only be detected  
30 in less than a half of the series covering more than one year. This would limit the analysis at  
31 the cost of generalisation. We thus decided to ignore the inter-annual component of the



1 variability and use annual composites of the entire time series for further analyses. This  
2 ensures that all datasets, irrespective of their duration and resolution, are treated uniformly. In  
3 multi-year series, such analysis alleviates the problem of uneven sampling and allows the use  
4 of all data despite sampling gaps.

5  
6 The sinusoidal representation of the seasonal shell flux pattern imposed by the periodic  
7 regression, describes the variance in the annual composite data to varying degrees (see Fig. S2  
8 for all fitting results). The maximum adjusted coefficient of determination for the periodic  
9 regression is 0.88 (*G. bulloides* at site 3) and the minimum coefficient still considered  
10 significant is 0.03 (*G. uvula* at site 33). On average, the periodic regression model explains  
11 more than one third of the variance, confirming that most of the flux series have a substantial  
12 periodic seasonal component. Irrespective of the regression coefficient, the difference  
13 between observed and estimated peak timing is small (mean error: -7 days; Fig. 2 and S3 for  
14 individual species), with most of the differences being within the average resolution of the  
15 time series. Nevertheless, there seems to be a tendency by the periodic regression to  
16 overestimate the timing of the peak (Fig. 2). Although the amount is below the resolution of  
17 most time series, this small bias may reflect an asymmetry in the peak flux pattern with higher  
18 fluxes following but not preceding the peak.

19  
20 With respect to the amplitude of the seasonal signal, the amplitude estimated by the periodic  
21 regression is always smaller than the observed amplitude (Fig. S2), which simply reflects the  
22 nature of the least-squares regression. In fact, even the raw data are unlikely to reflect the  
23 actual amplitude of the seasonal flux because of time averaging of the sampling. Especially in  
24 the presence of different time resolution and gaps the estimate based on periodic regression is  
25 likely to be more robust. Within the limitations described above, the general performance of  
26 the periodic regression is satisfactory and allows for objective characterisation of the seasonal  
27 shell flux patterns.

### 28 **3.2 Seasonality in shell flux**

29 The periodic regression analysis indicates the presence of a statistically significant cyclic  
30 component in more than 80 % of the annual composite flux series (table 2, Fig. S2). Of those  
31 cases, the majority is characterised by a single yearly flux peak. Only a single site (nr. 30, off

1 Brazil) completely lacks predictable seasonality. Other than a weak tendency for a smaller  
2 incidence of seasonality in the tropics, there is no strong pattern in the prevalence of  
3 seasonality with latitude or with annual temperature (Fig. 4A, B). The proportion of seasonal  
4 patterns characterised by two cycles per year seems to be higher at the extremes of the  
5 temperature range (Fig. 4A) and flux series with double cycles appear to be more frequently  
6 found in the Pacific Ocean (Fig. S5). The seasonal temperature range does not appear to show  
7 a relationship with the occurrence of seasonality in the shell flux, nor with the number of  
8 cycles characterising the seasonal pattern (Fig. 4C).

9

10 The peak prominence in flux series with a significant seasonal component varies between -2  
11 and 2, indicating differences in the peak flux over the mean flux by four orders of magnitude.  
12 At low latitudes seasonal shell flux patterns are characterised by generally low peak  
13 prominence and the proportion of patterns with intermediate peak prominence (-1 to 0)  
14 decreases with latitude (Fig. 4D). Fig. 4E shows that indeed warm-water sites are  
15 characterised by relatively low peak prominence, but at low temperature peak prominence is  
16 more variable and shell flux patterns with even lower peak prominence are observed in cold  
17 waters. The seasonal temperature range seems not to be a predictor of peak prominence (Fig.  
18 4F).

19

20 A significant seasonal component was found in the flux data for all 23 species analysed. In  
21 four species, significant cyclicity was only observed at <5 sites (Table 2). To avoid a bias due  
22 to low observation density, these species were excluded from analyses of species-specific  
23 patterns. As temperature is known to be an important predictor of zooplankton phenology  
24 (Mackas et al., 2012; Richardson, 2008) we initially compared the patterns of seasonality  
25 (peak timing and peak prominence) to mean annual temperature at each site averaged over the  
26 upper 50 m. By examining the relationship with temperature of the proportion of annual flux  
27 patterns with two cycles per year, peak timing and peak prominence, we were able to identify  
28 three groups of species with distinct modes of seasonality (Fig. 5). A particularly strong  
29 discriminator seems to be the relationship between peak prominence and temperature (see PP'  
30 in Fig. 5) and the presence of a systematic shift in peak timing with temperature. The  
31 behaviour of the species belonging to each group seems independent of the ocean basin and  
32 the presence/absence of upwelling (Fig. 5, Fig. S6).

### 1 **3.2.1 Tropical and subtropical species (Group A)**

2 This group comprises *G. ruber* (white and pink varieties), *N. dutertrei*, *G. sacculifer*, *O.*  
3 *universa*, *G. siphonifera*, *P. obliquiloculata*, *G. menardii*, *G. rubescens*, *G. tenella* and *G.*  
4 *conglobatus*. These species are characterised by a pattern best illustrated by *G. ruber* (white)  
5 and *G. sacculifer*, where peak timing varies randomly in warm waters ( $> 25\text{ }^{\circ}\text{C}$ ; Fig. 5A) and  
6 in colder waters becomes more focused in autumn. Species such as *P. obliquiloculata* and *G.*  
7 *menardii* that have a restricted high temperature range do not show this latter characteristic  
8 (Fig. S6). The focussing of peak timing to autumn in these species is associated with a clear  
9 increase in PP towards colder waters (Fig. 5). In the group as a whole, the temperature  
10 dependence of PP, expressed as the slope of a linear regression between PP and temperature,  
11 is negatively correlated with the mean temperature where the species is observed in our  
12 compilation ( $T_{\text{spec}}$ ) and positively with temperature range ( $\Delta T_{\text{spec}}$ ) ( $r^2 = 0.6$  and  $0.9$ ,  
13 respectively, excl *P. obliquiloculata*; Fig. 6B, D). In addition, for a given  $T_{\text{spec}}$ , these species  
14 show a low proportion of flux series with two cycles per year (table 2) and this proportion  
15 generally increases with temperature (Fig. 6A, C and S7) such that species observed in  
16 warmer waters (and observed within a narrower temperature range) have proportionally more  
17 double cycles ( $r^2 = 0.7$ ; Fig 6, C).

### 18 **3.2.2 Temperate and cold water species (Group B)**

19 *Globigerina bulloides*, *G. glutinata*, *N. incompta*, *N. pachyderma*, *G. scitula*, *G. calida*, *G.*  
20 *falconensis*, *G. theyeri* and *G. uvula* form the second group. These species show a flux pattern  
21 best represented by *G. glutinata* (Fig. 5), with two possible peak timings per year, both  
22 shifting towards later in the year towards lower temperature (Fig. 5B). In contrast to group A,  
23 the proportion of records with double cycles seems to decrease with temperature in this group  
24 (Fig. S7). In some cases a third, intermediate peak time, showing a similar trend with  
25 temperature, is visible (*G. scitula*, *G. bulloides*) and in other cases (e.g. *N. pachyderma*) the  
26 trends are not as clear (Fig. S5). None of these species shows a clear trend in peak  
27 prominence with temperature ( $\text{PP}' \sim 0$ ; Fig. 6; table 2). And with the exception of *G. scitula*  
28 and *G. falconensis*, the average PP of species in the group lies within a narrow range around -  
29 0.9 (table 2) and is not related to temperature across the species in the group (Fig. 6). For any  
30 given  $T_{\text{spec}}$ , the species show a higher proportion of series with two cycles per year than in

1 group A (fig. 6), but similar to group A, the proportion of double cycles increases with  $T_{\text{spec}}$   
2 and  $\Delta T_{\text{spec}}$  ( $r^2 = 0.7$  and  $0.6$  respectively, excl. *G. scitula*; Fig. 6A, C).

### 3 **3.2.3 Deep dwellers (Group C)**

4 This group consists of two species: *G. inflata* and *G. truncatulinoides*. Compared to the other  
5 groups, the proportion of flux series that showed only a single cycle per year is highest; only a  
6 single time series with two cycles per year is observed (table 2). The peak timing in both  
7 species is independent from temperature and occurs everywhere in winter, early spring (Fig.  
8 5C). Peak prominence is high (mean 0.07) and these species are the only ones indicating a  
9 positive PP' (Fig. 5C, Fig. 6, table 2).

10

## 11 **4. Discussion**

12 Our global compilation of shell flux time series from sediment traps shows that spatially  
13 variable seasonality is a ubiquitous and widespread phenomenon in planktonic foraminifera.  
14 Seasonality characterises the majority of the time series investigated at any latitude or  
15 temperature (range). The amplitude of the seasonal cycle and hence the effect of seasonality  
16 on the sedimentary record varies, however, among species, and with temperature. According  
17 to their seasonality pattern, the studied species can be classified into three groups.  
18 Importantly, this division holds for every ocean basin and is not affected by upwelling. This  
19 suggests that these groups reflect three principal modes of seasonality. Tropical and  
20 subtropical mostly symbiont-bearing species (group A) seem to adjust the peakedness of their  
21 seasonal flux pattern and do not change the timing of the peak flux. Temperate and cold-water  
22 species (group B) show the opposite and only shift the timing of peak flux during the year  
23 without changing the peak prominence. Deep dwellers have approximately constant peak  
24 timing and change the shape of the flux pattern, but in the opposite direction as group A.  
25 Indeed, the direction of the PP change with temperature/ sign of PP sensitivity (sign of PP') is  
26 the most robust discriminator between the three groups (Fig. 6).

27

28 Although the analysis revealed a high prevalence of a predictable component in the seasonal  
29 flux patterns, the periodic sinusoidal models used to detect and characterise seasonality only  
30 explained on average one third of the variability in the data. This may suggest that a  
31 significant part of the observed variability in the flux is not predictable. The additional

1 variability may reflect small differences in flux timing among years, high-frequency  
2 variability such as lunar cycles, long-term trends, non-periodic events or random noise. In  
3 addition, the scatter in the data may, at least in part, also be due to the nature of the flux  
4 observations itself.

5  
6 Several studies have shown that sediment traps moored at the same position but at different  
7 depths may record different shell fluxes (e.g. Curry et al., 1992; Mohiuddin et al., 2004). Such  
8 differences could be due to dissolution in the water column (Thunell et al., 1983), (lateral)  
9 advection of shells from different areas (Von Gyldenfeldt et al., 2000) or temporal lags  
10 reflecting the settling time of the shells (Takahashi and Bé, 1984). We have tried to use  
11 always the uppermost trap in order to minimise these effects, but it is impossible to exclude  
12 the possibility that part of the observed noise in the timing and strength of species flux is due  
13 to processes that have modified the primary export flux. However, the magnitude of this error  
14 is probably within the same range as for inter-annual variability and therefore within the range  
15 of error of the periodic regression approach. For instance, for settling speeds, studies have  
16 shown that depending on shell weight, size and shape, sinking speeds can vary over two  
17 orders of magnitude (Takahashi and Bé, 1984; Von Gyldenfeldt et al., 2000). For the deep  
18 traps, settling times could thus be as little as four days or as much as one month. This would  
19 introduce a unidirectional temporal offset from the primary signal near the ocean surface and  
20 the delivery of the flux to the sediment trap, the size of which would vary with trap depth and  
21 shell size. However, the temporal offset thus caused is within the uncertainty caused by  
22 applying the periodic regression (Fig 2). Similarly, large seasonal changes in the catchment  
23 area and differential dissolution during settling would have most affected the deepest traps.  
24 However, because of our preference for shallower traps (only two of the analysed records are  
25 from traps moored deeper than 4000 m and only 11 of the 37 traps were moored deeper than  
26 3000 m; Table 1), this effect is probably small.

27  
28 Moreover, small but consistent differences in seasonality of shell flux in different size classes  
29 have been reported (Jonkers et al., 2013; Thunell and Reynolds, 1984). The data presented  
30 here are mostly from the >125 or >150  $\mu\text{m}$  fraction and the fraction analysed was always held  
31 constant within each trap series. As a result, the effect of size differences on the observed  
32 phenology is probably limited. In contrast, the magnitude of the shell flux is more size

1 dependent. Since small shells tend to be more abundant (Berger, 1969), the inclusion of  
2 smaller sized shells could cause large changes to the amplitude of flux variation. However,  
3 including smaller specimens would also increase the background flux and by normalising the  
4 amplitude to the mean flux (peak prominence) we have largely excluded the size effect when  
5 comparing data from different records.

6

7 Next, this compilation includes assemblage counts carried out by many different researchers.  
8 Consequently, complete taxonomic consistency between all the different studies cannot be  
9 guaranteed. This may in particular hold for the *Neogloboquadrinids* in the Pacific, where  
10 different coiling directions are distinguished in both *N. incompta* and *N. pachyderma*  
11 (Kuroyanagi et al., 2002). Furthermore, analytical errors resulting from counting and splitting  
12 have to our knowledge never been properly quantified, but are probably minimal compared to  
13 the size of the seasonal signal and are almost certainly random.

14

15 Even if one would assume that the flux time series are a robust representation of the flux  
16 pattern of each species as it occurred at the year of collection, the interpretation of the  
17 observed patterns could be obscured by the existence of genetic diversity within species. The  
18 analysed shell flux data are based on morphospecies and many of those include multiple  
19 distinct genetic lineages (“cryptic species”), which might have distinct ecological habitats and  
20 may be endemic to separate ocean basins or regions (e.g. Darling et al., 2007). If the  
21 phenology of the constituent cryptic species were different, the patterns based on  
22 morphological species may be spurious. However, the observed modes of seasonality appear  
23 to be independent of ocean basins (Fig. 5, S6) and display consistent features among different  
24 species. This suggests that the seasonality of cryptic species is similar within one  
25 morphospecies. Apparently, ecophysiological differences between morphospecies could be  
26 responsible for some noise in the data, but are too small to change the attribution to one of the  
27 three groups. This is consistent with the three main modes of seasonality occurring across  
28 different taxa, reflecting a functional aspect of species ecology and their environment rather  
29 than their taxonomic attribution.

#### 1 **4.1 Environmental controls on shell flux seasonality**

2 Temperature exerts a major influence on the spatial distribution of planktonic foraminifera  
3 species (Bé and Tolderlund, 1971; Morey et al., 2005) and it is likely that the temporal  
4 distribution (seasonality) is likewise influenced by temperature. Indeed, in other groups of  
5 zooplankton temperature appears to be the best predictor of phenology (e.g. Mackas et al.,  
6 2012; Richardson, 2008), although the exact mechanism by which temperature controls  
7 phenology is not fully understood (Mackas et al., 2012). The three different modes of  
8 seasonality we identified in planktonic foraminifera also indicate that different species  
9 respond differently to changing environmental parameters and a potential temperature effect  
10 is complex.

11  
12 Temperature can affect zooplankton phenology in different ways (Mackas et al., 2012). It  
13 could directly affect phenology through acceleration of metabolic processes. Such a direct  
14 physiological effect may be what drives, or contributes to, the earlier when warmer pattern in  
15 the species of group B. However, in some groups of zooplankton the observed changes in  
16 seasonality are larger than expected from the metabolic effect of temperature alone, rendering  
17 such a direct temperature control unlikely (Mackas et al., 2012). Moreover, shell growth and  
18 survival appear to reach a saturation level at given temperatures in planktonic foraminifera  
19 (Bijma et al., 1990), above which temperature could not have any direct effect on flux.

20 Consequently, a direct temperature effect is unlikely to fully explain the observed seasonal  
21 behaviour amongst the different species.

22 An alternative explanation for the effect of temperature on seasonality is that individual  
23 species have a thermal niche: a preferred temperature range with an optimal balance between  
24 growth and respiration. Reproductive success would then simply follow temperature, leading  
25 to the observed seasonality in the shell fluxes (e.g. Lombard et al., 2011; Zaric et al., 2005).

26 This explanation also takes into account the differences in the temperature zonation among  
27 species (Bé and Tolderlund, 1971) and is confirmed by observations of a relationship between  
28 highest abundance and largest sizes (Hecht, 1976). It is therefore probably a better mechanism  
29 to explain the role of temperature than a direct metabolic control.

30 Finally, temperature may simply serve as a predictor or cue of optimal conditions (Mackas et  
31 al., 2012). This would imply that species use (changes in) temperature as an indication of  
32 favourable conditions to time their reproduction, rather than there being any (in)direct

1 advantages associated with a certain temperature range. Such a “signalling” role of  
2 temperature is important for reproduction timing in organisms living in seasonally variable  
3 environments, which are depending on correctly anticipating the arrival of optimum  
4 conditions for their offspring.

5 It is important to note, however, that in large parts of the ocean temperature is correlated to a  
6 number of other parameters, including factors that control phytoplankton productivity.

7 Consequently, it remains difficult, in part due to the lack of data on these correlates, to assess  
8 if temperature really is the most important factor in determining the seasonality in planktonic  
9 foraminifera (or in zooplankton in general), or whether the correlation between temperature  
10 and seasonality is a statistical artefact.

#### 11 **4.1.1 Warm-water species**

12 With the exception of *G. siphonifera* and *O. universa*, species in this group have relatively  
13 narrow and warm thermal optima above 20 °C (Bé and Tolderlund, 1971; Zaric et al., 2005).

14 At high temperatures the flux is relatively even throughout the year (low PP) and peak timing  
15 appears to be distributed throughout the year (Fig. 5, S6). Nevertheless, even at the warmest  
16 sites, the periodic regression indicates a significant seasonal component, often with two  
17 cycles per year, in the flux series of these species. Despite the low amplitude of the observed  
18 flux seasonality, the periodic model often explains a large portion of the variance in the data  
19 (e.g., 40% for *G. ruber* (white) at site 31 in the Mozambique Channel or over 50% for several  
20 species at site 27 in the South China Sea). However, we note that almost all of the tropical  
21 sites are affected by local seasonal change in environmental conditions, in each case reflecting  
22 different processes, such as the monsoon in South China Sea and the Arabian Sea, upwelling  
23 in Cariaco Basin and off Java. It seems that these processes are sufficiently strong to pace the  
24 flux of planktonic foraminifera species at most locations in the tropics, but the resulting  
25 seasonal pattern has a relatively low amplitude.

26

27 With decreasing temperature, the flux pattern of these warm-water species becomes more  
28 predictable: the peak prominence increases and peak timing is progressively focussed towards  
29 the autumn (Fig. 5, S6). This behaviour can be explained by the existence of a species-  
30 specific thermal optimum. In tropical areas, optimum temperatures occur year-round, whereas  
31 outside the tropics, they occur only for a short duration during the warm season.



1 Consequently, these species concentrate a larger proportion of the annual flux in a shorter  
2 period (increase PP). Species showing a more restricted tropical preference show a higher  
3 PP', indicating that the tendency to concentrate the flux is greater in species with a narrow  
4 high temperature habitat (Fig. 6). Interestingly, with decreasing temperature, only *N. dutertrei*  
5 shifts its maximum flux to the period of maximum temperature, whereas the other species  
6 seem to time the flux peak to one to two months after the temperature peak (Fig. 7, S8). This  
7 may reflect different growth rates among these species, with *N. dutertrei* having a higher  
8 fecundity or a shorter generation time. The cessation of the peak flux would then represent a  
9 thermal barrier to reproduction or growth. In this way, the observed pattern would represent  
10 strong evidence for the existence of a thermal niche in these species.

11  
12 The presence of symbionts in this group is in line with the dominant temperature control on  
13 the seasonal flux pattern of these species. With the exception of *G. rubescens*, which was  
14 never under systematic investigation, all other species in this group have been found in  
15 association with algal endosymbionts (Gastrich, 1987; Spindler and Hemleben, 1980), which  
16 decrease their reliance on primary productivity. To test this hypothesis, we compared the  
17 timing of maxima in surface chlorophyll concentration with maxima in the shell flux (Fig. 8).  
18 This analysis reveals a wide and relatively even distribution of temporal offsets between peak  
19 flux and peak productivity, indicating no relationship between these variables. Although the  
20 number of cases is relatively small, it is possible to evaluate the association between shell flux  
21 and productivity quantitatively. To this end, we consider a peak in the flux as coinciding with  
22 a chlorophyll maximum as long as the peak flux occurs within 49 days before to 79 days after  
23 the chlorophyll maximum. This interval is chosen to account for the uncertainty due to  
24 discrete observations of shell flux (average resolution of 19 days) and the chlorophyll data  
25 (resolution of 1 month), adding a plausible lag between foraminifera response to productivity  
26 of 1 month. This analysis reveals a possible statistically significant association between shell  
27 flux and productivity (c.i. 95%; binomial test) only for *G. siphonifera* and *P. obliquiloculata*,  
28 where it is driven by observations from upwelling sites, showing a negative lag within the  
29 uncertainty interval.

#### 1 **4.1.2 Temperate and cold water species**

2 Most species that are typically associated with temperate to cold water conditions show two  
3 possible flux peak timings per year and exhibit a tendency to shift their peak(s) to earlier in  
4 the year at higher temperatures (Fig. 5B). Such an earlier-when-warmer trend is widely  
5 observed in other (zoo)plankton groups (Mackas et al., 2012). In this group, temperature  
6 appears to affect the timing of both flux peaks and the earlier-when-warmer pattern suggests a  
7 temperature control on the peak timing in this group. However, a direct metabolic control on  
8 peak timing is unlikely, because both seasonal flux peaks in these species do not coincide  
9 with temperature maxima. Alternatively, if the species would have a clearly defined thermal  
10 niche, it would be expected that peak fluxes occur everywhere approximately within this  
11 temperature range (but at different times in the year). However, peak fluxes in the temperate  
12 to cold-water species occur over a wide temperature range (>20 °C for some species; e.g. *G.*  
13 *bulloides* and *G. glutinata*, see Fig. 7, S8). This indicates that the existence of species-specific  
14 thermal niches is unlikely to explain the earlier-when-warmer patterns. In fact, this is in  
15 agreement with the wide temperature tolerance for most of these species (Tolderlund and Bé,  
16 1971; Zaric et al., 2005). Consequently, we entertain to possibility that the relationship  
17 between temperature and peak timing could stem from a correlation between temperature and  
18 the actual determinant of shell flux.

19  
20 The presence of two cycles (blooms) per year, one in spring and a second after breakdown of  
21 the summer stratification, is also a common feature of phytoplankton blooms at mid latitudes  
22 (e.g. Edwards and Richardson, 2004). The timing of these blooms is to some degree  
23 dependent on temperature and an association of peak flux in the species of this group with  
24 productivity is thus a plausible candidate mechanism. A reliance on productivity in this group  
25 is also consistent with the lack of symbionts in most of its species. The presence of symbionts  
26 has been suggested for *G. falconensis*, *G. glutinata* and *T. quinqueloba*. However, Gastrich  
27 (1987) did not observe algal symbionts in *G. falconensis* and the suggestion of symbionts in  
28 this species mentioned in Spero and Parker (1985), derives from misidentification of this  
29 species (Spero, personal communication 2014). In addition, the presence of symbionts in *T.*  
30 *quinqueloba* is mentioned in the description of this species in Hemleben et al. (1989), but no  
31 information is provided on the origin of this observation. Only in *G. glutinata* an association  
32 with symbionts is supported by direct observations (Gastrich, 1987).

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Having identified productivity as a potential factor controlling the flux phenology in temperate to cold-water planktonic foraminifera species, we compared the timing of maxima in surface chlorophyll concentration with maxima in the shell flux following the same approach as in the warm-water species (Fig. 8). Indeed, most species in this group show an association between the timing of peak flux and chlorophyll maxima. Only in *G. calida* and *G. scitula*, the association is not statistically significant and *G. falconensis* has a too small a number of observations. The dominance of a significant relationship between the timing of shell flux and chlorophyll maxima supports previous studies that indicated a link between productivity and shell flux in the temperate species (Hemleben et al., 1989; Schiebel et al., 1997). Thus, our analysis suggests that the timing of primary productivity serves as a predictor of peak flux timing in the temperate to cold-water species.

#### 4.1.3 Deep dwelling species

Of the three deep-dwelling species analysed, two appear to show a unique pattern of seasonality, distinct from both groups described above. Whereas *G. scitula* shows a pattern consistent with group B, the peak flux of *G. truncatulinoides* and *G. inflata* is observed around the same time in winter or spring (Fig. 5C) and a large proportion of the annual flux occurs in a single high-flux pulse (high PP, low % double cycles; table 2). Both characteristics might relate to a longer life cycle, as proposed for *G. truncatulinoides* (Hemleben et al., 1989). The two species show a (weak) positive correlation between peak prominence and temperature (Fig. 5C), which could indicate higher year-round reproductive success at lower temperatures in agreement with the preferred peak timing around the coldest time of the year and also with their preferred temperature range (Bé and Tolderlund, 1971; Tolderlund and Bé, 1971). Alternatively, the more evenly distributed seasonal flux pattern outside the tropics could reflect a higher proportion of expatriated specimens that have higher mortality outside the peak flux period, but this does not agree with the higher abundance of both species at lower temperatures (Bé and Tolderlund, 1971; Tolderlund and Bé, 1971). As expected, because of the relatively constant timing of peak flux in both species, there is no association between the timing of their flux and that of productivity.

1 The peak shell flux around the coldest month during the year (clearest in *G. truncatulinoides*)  
2 argues against a direct metabolic influence of temperature on the peak timing. Similarly, if  
3 these species had a well-defined thermal niche between ~10 and 24 °C as suggested by (Bé  
4 and Tolderlund, 1971) one would expect that at both ends of that temperature range the peak  
5 flux would represent a larger proportion of the total annual flux because the seasonal growth  
6 window is become shorter. However, we do not observe such increase in the PP at the cold  
7 end of the temperature range (Fig. 5C). This argues against temperature controlling the  
8 seasonal pattern and suggests that either some correlated factors determine the seasonality in  
9 this group, or that the species use some feature of the seasonal temperature cycle as a cue to  
10 anticipate optimal conditions for their offspring. Although both species are considered deep  
11 dwellers, they migrate vertically through the water column and spend a significant part of  
12 their life cycle relatively close to the sea surface (Field, 2004; Loncaric et al., 2006;  
13 Tolderlund and Bé, 1971). Thus, the trigger for the regular flux pulse could originate from  
14 conditions close to the surface, where seasonal environmental changes tend to be of higher  
15 magnitude.

#### 16 **4.2 Paleoceanographic implications**

17 The existence of a significant seasonal component in the shell flux pattern of extant  
18 planktonic foraminifera has implications for the interpretation of the fossil record. Since  
19 seasonality is species-specific and spatially variable, fossil assemblages of the same species  
20 collected at different locations contain in the composition of their shells a different amount of  
21 seasonal bias. Firstly, this may affect proxy calibrations based on sediment core tops, which  
22 depending on their location will reflect a variable amount of seasonal bias and not reflect  
23 mean annual conditions. Because of such seasonal bias, determining the environmental niche  
24 of a certain species using mean annual conditions leads to an overestimation of the width of  
25 this niche. Consequently, under these assumptions, calibration based on mean annual  
26 environmental conditions may not be meaningful. Hönisch et al. (2013) provide an instructive  
27 example on how seasonality may affect Mg/Ca-temperature calibration, but seasonal biasing  
28 may also affect multivariate biotic approaches based on foraminiferal assemblages.  
29 Secondly, this spatial bias may translate into a temporal bias in records straddling climatic  
30 transitions. The size of the bias is a function of the amplitude of the seasonal cycle (PP), the  
31 variance in the timing of peak flux and the inter-annual amplitude of the change in the

1 environmental parameter to be reconstructed. Our compilation of shell flux time series allows  
2 an assessment of the potential size of such a bias in the fossil record by calculating a flux-  
3 weighted average temperature for a synthetic sample that would be deposited below the  
4 location of each trap. Fig. 9 shows the spatial distribution of the seasonal bias within each  
5 species expressed as a difference between the flux-weighted temperature and the mean annual  
6 temperature (0-50 m water depth). Species-specific depth habitats were not taken into account  
7 in the calculation of these offsets, which likely leads to an overestimation of the size of the  
8 bias for deep dwelling species. If the flux of a species is even throughout the year or the  
9 temperature does not vary, the offset would tend to zero. If the flux shows peaks of similar  
10 size and constant timing, the offsets for one species will always have the same sign. In all  
11 other cases the distribution of the bias will be more complex, precluding generalisations, such  
12 as a classification to summer or winter species.

13 The temperature offsets due to seasonality vary between +4 and -4 °C and may range by as  
14 much as 6°C within one species (Fig. 9). At a single location, species with a different  
15 seasonality mode may show different flux-weighted offsets. This is more likely to occur at  
16 intermediate temperatures where warm and cold-water species mix and has been observed  
17 previously (Jonkers et al., 2013; King and Howard, 2005). Large positive offsets are generally  
18 found at higher latitudes, reflecting a preference for summer flux in colder regions. As a result  
19 of the earlier-when-warmer trend in peak timing, negative offsets are observed in temperate  
20 zones in many species of group B. The offsets are often larger than the uncertainty of Mg/Ca  
21 temperature estimates (about 1°C; Anand et al. (2003)) and translate to an approximately 2 ‰  
22 range in  $\delta^{18}\text{O}$ . This means the present-day spatial pattern in temperature offsets due to varying  
23 flux seasonality within a species could be large enough to explain the magnitude of glacial-  
24 interglacial change in most parts of the ocean (MARGO project, 2009). Indeed, seasonality  
25 has been invoked as a possible explanation of the observed discrepancy between Mg/Ca  
26 paleotemperatures, other paleothermometers and climate models (Laepple and Huybers, 2013;  
27 Leduc et al., 2010; Lohmann et al., 2013).

28 In addition, changes in the shape of the seasonal flux pattern, particularly in the peak  
29 prominence, could influence the variability in proxy records. A seasonal flux pattern with  
30 higher PP means that the foraminifera register ambient seawater conditions during a shorter  
31 interval in the year and this will result in a narrower distribution of individual shell signatures  
32 in the sediment. This not only reduces intra-sample variability, but since only a small fraction

1 of the total number of foraminifera is used for analysis, also the variability between samples  
2 (Laepfle and Huybers, 2013).

3 Both effects clearly illustrate the importance of seasonal variation in shell fluxes on the fossil  
4 record and the need to take potential transient changes in seasonality into account.

5 Importantly, a transient change in the seasonal bias as a result of changing environmental  
6 factors will depend on the mode of seasonality that characterises the species. Thus, although  
7 the magnitude of the temperature offsets due to seasonality is large within species (Fig. 9), in  
8 reality, the presence of the distinct seasonality modes means that the expected bias through  
9 time due to shifting seasonality varies predictably in its sign and magnitude.

10

11 Within the optimal temperature range of warm-water species, seasonal variation in the shell  
12 flux is low and these species thus record average annual conditions with very little offset (Fig.  
13 9). However, outside their optimum temperature range, these species concentrate a  
14 progressively larger portion of their annual flux into a single peak in autumn, leading to an  
15 increasingly positive bias from mean annual conditions. Consequently, during a cooling trend,  
16 the seasonality of these species would shift towards the summer and the proxies based on  
17 such species would underestimate the magnitude of the temperature shift. Conversely, during  
18 a warming trend, these species will shift their seasonality from dominantly autumn to a more  
19 even flux throughout the year, also leading to an underestimation of the actual change in mean  
20 temperature. The resulting intra-sample variability due to seasonality will remain similar, so  
21 single-shell analyses are unlikely to resolve this effect. Because of the observed pattern of  
22 shifting peak timing at present, temperate and cold-water species are most likely to exhibit  
23 transient changes in seasonality. As is the case in group A, a shift in seasonality during  
24 climate transitions will lead to an underestimation of the actual environmental changes  
25 reconstructed using these species. During a warming trend, these species will shift the peak  
26 timing towards earlier in the year recording lower temperatures and vice versa. Finally, the  
27 fossil record of deep-dwelling species predominantly reflects late winter/spring conditions.  
28 However, as the peak prominence in this group increases with temperature, this seasonal bias  
29 is larger at higher temperatures. Thus, during a warming trend, more of the flux is focussed in  
30 the narrow seasonal peak and the species records lower temperature, underestimating the  
31 amplitude of temperature change. During a cooling trend, the flux is less focussed recording  
32 on average warmer conditions. Thus, remarkably, despite the three principle modes of

1 seasonality, transient changes in seasonality always result in an underestimation of the  
2 amplitude of environmental change recorded in fossil foraminifera.

3

4 The recognition of the existence of distinct modes of seasonality in planktonic foraminifera  
5 provides an important perspective for validation of planktonic foraminifera growth models  
6 (Fraile et al., 2009a; Lombard et al., 2011; Zaric et al., 2006). Rather than validating models  
7 by evaluating their performance at individual sites, it should be possible to diagnose whether  
8 the model representation of individual species is consistent with their observed seasonality  
9 mode. Alternatively, the observed seasonality patterns can be used to guide model  
10 development. For example, the strong relationship between PP and mean annual temperature  
11 in group A combined with the tendency to shift peak time towards autumn, should be  
12 relatively easy to parametrise and implement, potentially allowing a more powerful prediction  
13 of the effect of seasonality on the fossil record of species in this group. Similarly, in group B,  
14 peak timing shows a strong association with productivity. Primary productivity is in some  
15 models explicitly simulated (e.g. Henson et al., 2009), offering the chance to predict changes  
16 in seasonality of species in this group from the seasonality of primary production. A  
17 combination of models with realistic representation of species seasonality with proxy data  
18 certainly holds the best potential to estimate the actual amplitude of past environmental  
19 change recorded in shells of planktonic foraminifera.

## 20 **5. Conclusions**

21 Our systematic overview revealed that all 23 species of planktonic foraminifera studied have  
22 a predictable cyclic component in the intra-annual variability in their shell fluxes. This  
23 seasonality is spatially variable within individual species and, depending on the species,  
24 predominantly driven by temperature or by primary productivity. We identified three groups  
25 of species with similar modes of seasonality:

- 26 1. Tropical and subtropical species (*G. ruber* (white and pink varieties), *N. dutertrei*, *G.*  
27 *sacculifer*, *O. universa*, *G. siphonifera*, *P. obliquiloculata*, *G. menardii*, *G. rubescens*,  
28 *G. tenella* and *G. conglobatus*) have relatively even flux patterns with low prominence  
29 peaks occurring at any time of the year in their optimum high temperature range (> 25  
30 °C). In colder waters peak fluxes become more prominent and focussed in autumn.  
31 This tendency is stronger in species with a narrow thermal range. The prevalence of  
32 endosymbionts in these species probably reduces their reliance on primary production

1 for food. Indeed, seasonality in this group appears to be primarily driven by  
2 temperature, suggesting the existence of a thermal niche for these species.

- 3 2. Temperate and cold-water species (*Globigerina bulloides*, *G. glutinata*, *N. incompta*,  
4 *N. pachyderma*, *G. scitula*, *G. calida*, *G. falconensis*, *G. theyeri* and *G. uvula*) show  
5 one or two cycles per year and peak flux timing occurs later in the year at lower  
6 temperature. Peak timing in this groups occurs at the same time or slightly after  
7 maximum chlorophyll concentration, suggesting a tight link between primary  
8 productivity and shell flux seasonality in these dominantly symbiont-barren species.
- 9 3. Deep-dwelling species (*G. inflata* and *G. truncatulinoides*) always reach peak flux in  
10 winter-spring independent of temperature and productivity, but concentrate a larger  
11 proportion of the annual flux in short period in warmer waters.

12 The environmental control on shell flux seasonality implies that changes in seasonality are  
13 likely to have occurred during past climate change, leading to a change in the seasonal bias in  
14 foraminiferal proxy records through time. Our analysis indicates that the effect of this  
15 changing seasonal bias leads to an underestimation of the change in mean conditions,  
16 irrespective of the seasonality mode. However, the recognition of the three principal modes in  
17 seasonality offers opportunities to test and improve foraminiferal growth models, ultimately  
18 allowing for improved reconstructions of climate change.

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1 Table 1: Details of shell flux time series used in this study. Site numbers refer to figure 1.

2

Site #	Lat [°N]	Lon [°E]	Depth [m]	Duration [days]	Size [µm]	Remarks	References
1	69.7	-0.5	500	780	63-500		(Jensen, 1998)
2	59.3	149.8	258	365	>150	<i>N. dutertrei</i> removed	(Alderman, 1996)
3	59.0	-38.5	2750	988	150-315	<i>T. quinqueloba</i> 150-250 µm	(Jonkers et al., 2010; Jonkers et al., 2013)
4	53.1	-177.0	3198	2926	>125		(Asahi and Takahashi, 2007)
5	50.0	165.0	3260	1141	>125		(Kuroyanagi et al., 2002)
6	50.0	-145.0	3800	1128	>125		(Sautter and Thunell, 1989)
7	49.0	-174.0	4812	2803	>125		(Asahi and Takahashi, 2007)
8	48.0	-21.0	2000-3700	378	>150	Depth change	(Wolfteich, 1994)
9	44.0	155.0	2957	851	>125		(Kuroyanagi et al., 2002)
10	43.0	5.2	500	3338	>150		(Rigual-Hernández et al., 2012)
11	42.4	3.5	500	3552	>150		(Rigual-Hernández et al., 2012)
12	42.0	155.2	1091	380	>125		(Mohiuddin et al., 2005)
13	40.0	165.0	2986	768	>125		(Kuroyanagi et al., 2002)
14	39.0	147.0	1371-1586	608	>125	Depth change	(Mohiuddin et al., 2002)
15	36.7	154.9	5034	376	>125		(Mohiuddin et al., 2004)
16	34.3	-120.0	590; 470	1108	>125	Depth change	(Darling et al., 2003; Kincaid et al., 2000)
17	34.0	-21.0	2000	378	>150		(Wolfteich, 1994)
18	33.0	22.0	3000	764	>125		(Storz et al., 2009)
19	32.1	-64.3	3200	1848	>125		(Deuser and Ross, 1989; Deuser et al., 1981)
20	27.5	-90.3	700	1563	>150		(Poore et al., 2013; Reynolds et al., 2013)
21	25.0	137.0	917-	573	>125	Depth change	(Mohiuddin et al.,

			1388				2002)
22	21.2	-20.7	3500	718	>150		(Fischer et al., 1996; Zaric et al., 2005)
23	16.3	60.5	3020	508	>125		(Curry et al., 1992)
24	15.5	68.8	2790	482	>125		(Curry et al., 1992)
25	14.5	64.8	732	486	>125		(Curry et al., 1992)
26	10.5	-65.5	Not reported	1002	>125		(Tedesco and Thunell, 2003)
27	9.4	113.2	720	662	>154		(Wan et al., 2010)
28	-7.5	-28.0	671	500	>150		(Zaric et al., 2005)
29	-8.3	108.0	1370-1860	963	>150	Depth change	(Mohtadi et al., 2009)
30	-11.6	-28.5	710	944	>150		(Zaric et al., 2005)
31	-16.8	40.8	2250	863	250-315		(Fallet et al., 2010; Fallet et al., 2011)
32	-20.0	9.2	1648	524	>150		(Zaric et al., 2005)
33	-30.0	-73.0	2300-2500	1563	>150		(Marchant et al., 2004; Marchant et al., 1998)
34	-46.8	142.0	3800	464	>150		(King and Howard, 2003)
35	-52.6	174.2	442; 362	410	>150	Depth change	(Northcote and Neil, 2005)
36	-62.5	-34.8	863	418	>125		(Donner and Wefer, 1994)
37	-64.9	-2.5	360	745	>125		(Donner and Wefer, 1994)

1

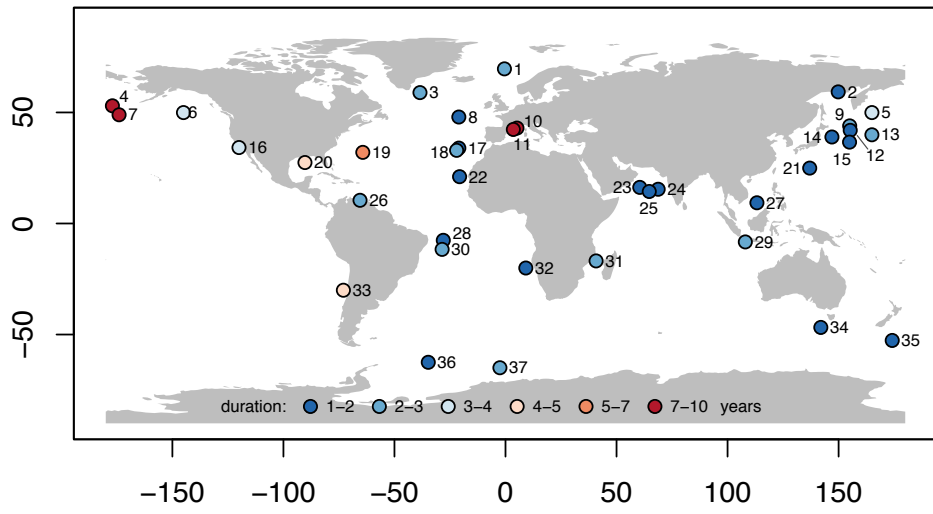
2

1 Table 2: Results from periodic regression. Species marked with an \* have <5 observations  
 2 with significant cyclicity and are excluded from the analysis.

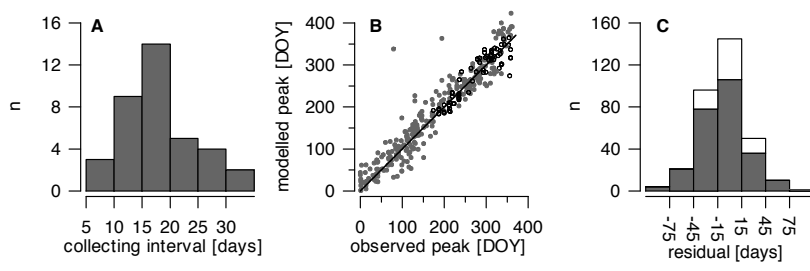
3

species	# in Fig. 6	# of time series	1 cycle	2 cycle	1 cycle [%]	2 cycle [%]	mean PP	PP' [ $^{\circ}\text{C}^{-1}$ ]
Group A								
<i>G. ruber</i> (white)	1	20	12	5	60	25	-0.91	-0.09
<i>N. dutertrei</i>	2	17	13	3	76	18	-0.36	-0.03
<i>G. sacculifer</i>	3	18	11	4	61	22	-0.64	-0.07
<i>O. universa</i>	4	18	10	2	56	11	-0.05	-0.06
<i>G. siphonifera</i>	5	17	4	4	24	24	-0.40	-0.06
<i>G. ruber</i> (pink)	6	8	5	2	63	25	-0.07	-0.14
<i>P. obliquiloculata</i>	7	8	3	4	38	50	0.00	-0.48
<i>G. menardii</i>	8	6	2	3	33	50	-0.74	-0.21
<i>G. rubescens</i>	9	6	3	2	50	33	-0.41	-0.17
<i>G. tenella</i> *	-	7	2	2	29	29	-	-
<i>G. conglobatus</i> *	-	5	1	1	20	20	-	-
Group B								
<i>G. bulloides</i>	10	32	22	9	69	28	-0.86	0.02
<i>G. glutinata</i>	11	25	13	8	52	32	-0.93	-0.01
<i>T. quinqueloba</i>	12	21	15	5	71	24	-0.94	0.01
<i>N. incompta</i>	13	22	12	5	55	23	-0.76	0.01
<i>N. pachyderma</i>	14	16	11	4	69	25	-0.91	0.00
<i>G. scitula</i>	15	18	10	2	56	11	-0.30	0.02
<i>G. calida</i>	16	9	4	3	44	33	-0.82	0.02
<i>G. falconensis</i>	17	6	4	2	67	33	0.14	0.01
<i>G. theyeri</i> *	-	5	2	2	40	40	-	-
<i>G. uvula</i> *	-	5	4	0	80	0	-	-
Group C								
<i>G. inflata</i>	18	13	10	1	77	8	0.15	0.08
<i>G. truncatulinooides</i>	19	12	9	0	75	0	-0.02	0.09
				Group average				
				A	51	29	-0.40	-0.14
				B	60	26	-0.67	0.01
				C	76	4	0.07	0.08

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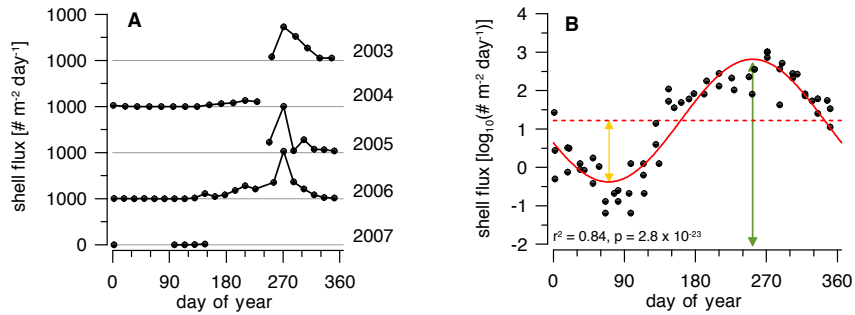
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 2 Fig. 1: Distribution and duration of sediment trap time series used in this study. Site numbers  
 3 refer to table 1.  
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2 Fig. 2: Histogram of average collecting interval for all time series (A). Observed vs modelled  
 3 peak time (B) and residual of observed- modelled peak time (C). See Fig. S3 and S4 for  
 4 individual species. Solid symbols in B and C denote single or first cycles and open symbols  
 5 second cycles.

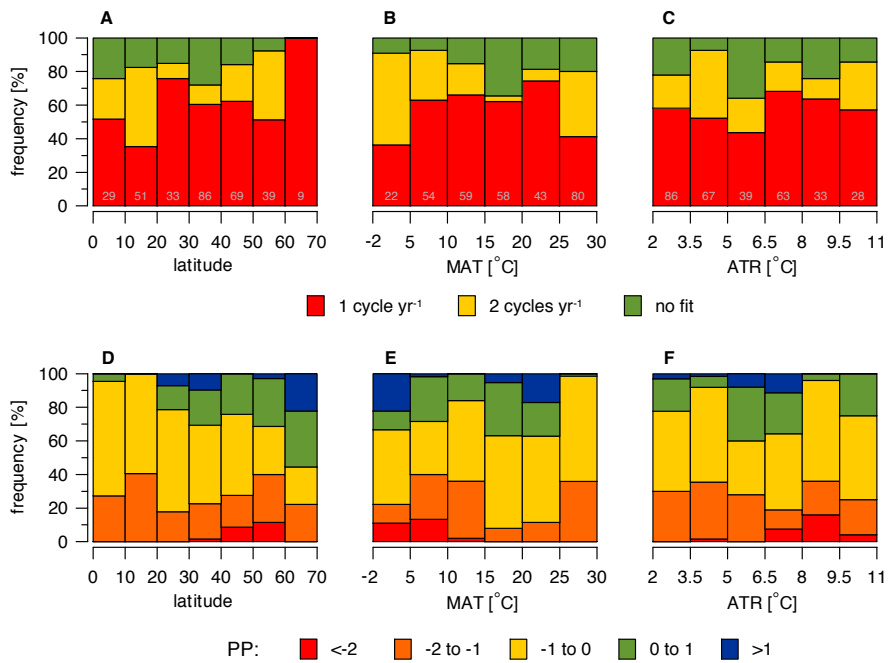
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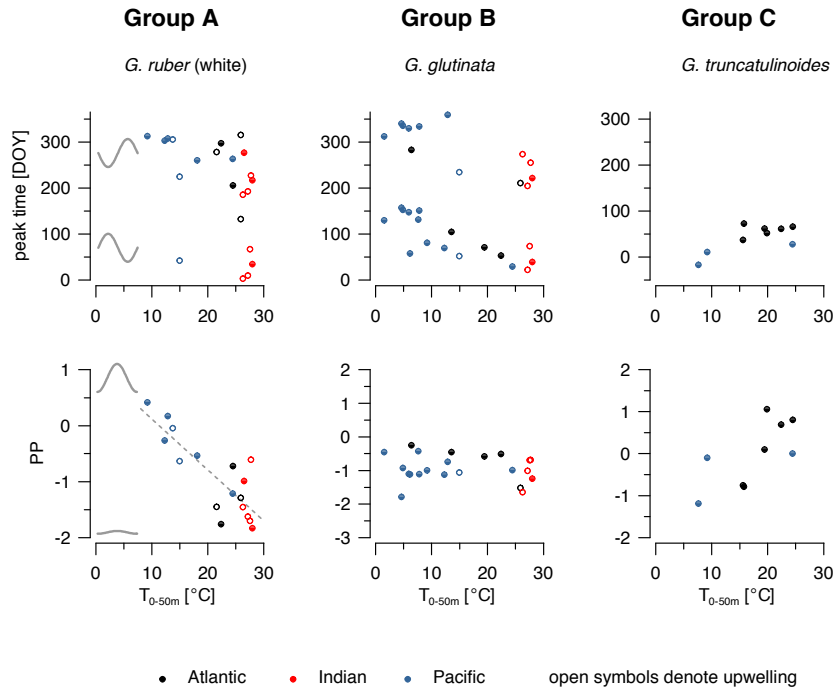
2 Fig. 3: Example of the periodic regression approach. A: raw data plotted vs yearday and at  
 3 mid dates of collection intervals. B: log-transformed data and fitting approach; the thick red  
 4 line represents the best fit for the two models tested. The dashed horizontal red line is the  
 5 periodic mean, the solid yellow arrow indicates the amplitude of the cycle and the green  
 6 arrow indicates the modelled peak time. Data are from *T. quinqueloba* from site 3.

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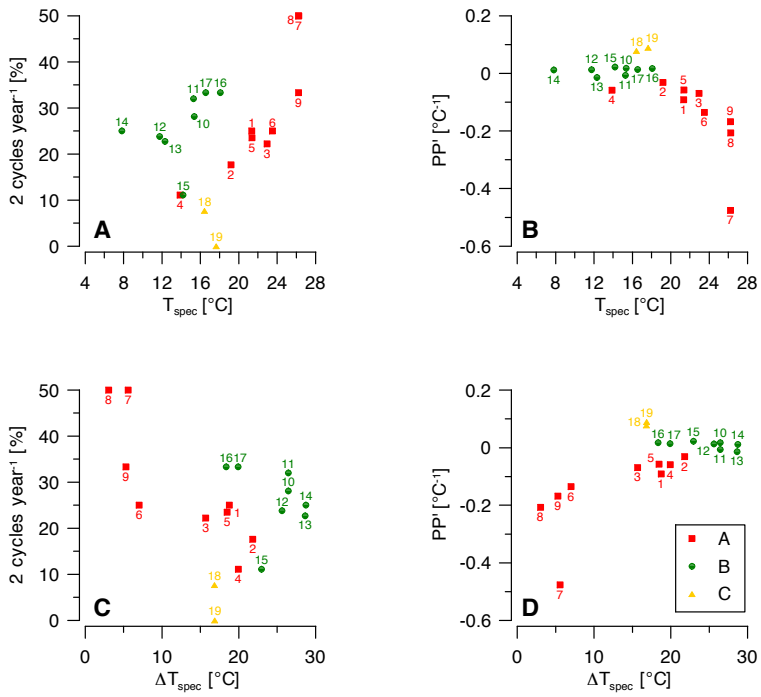
Fig. 4: General patterns in shell fluxes. Top row: proportion of annual shell flux patterns showing seasonality and those characterised by one or two cycles per year vs. absolute latitude (A), mean annual temperature (B) and annual temperature range (C). Numbers denote sample size (n). Bottom row: peak prominence distribution vs. same parameters as above.



1

2 Fig. 5: Three modes of seasonality: examples of each group, for all species see Fig. S6. Peak  
 3 timing (day of year (DOY) on NH scale) and peak prominence (PP) vs. mean annual  
 4 temperature between 0 and 50 m. Group A: warm-water, symbiont-bearing species. Group B:  
 5 temperate and cold-water species. Group C: deep-dwellers. The grey solid curves in A  
 6 illustrate the peak timing and prominence and the dashed grey line highlights the linear  
 7 relation between PP and temperature (PP'). Note that peak timing represents circular data and  
 8 that for *G. truncatulinoides* peak timing close to DOY 365 has been plotted as a negative  
 9 value to highlight the pattern.

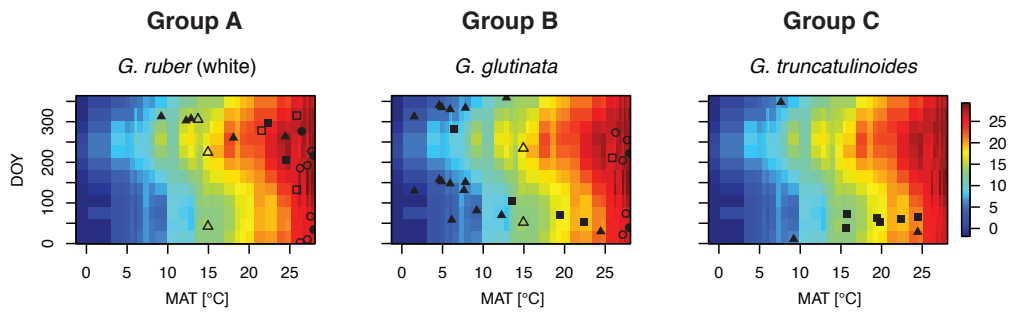




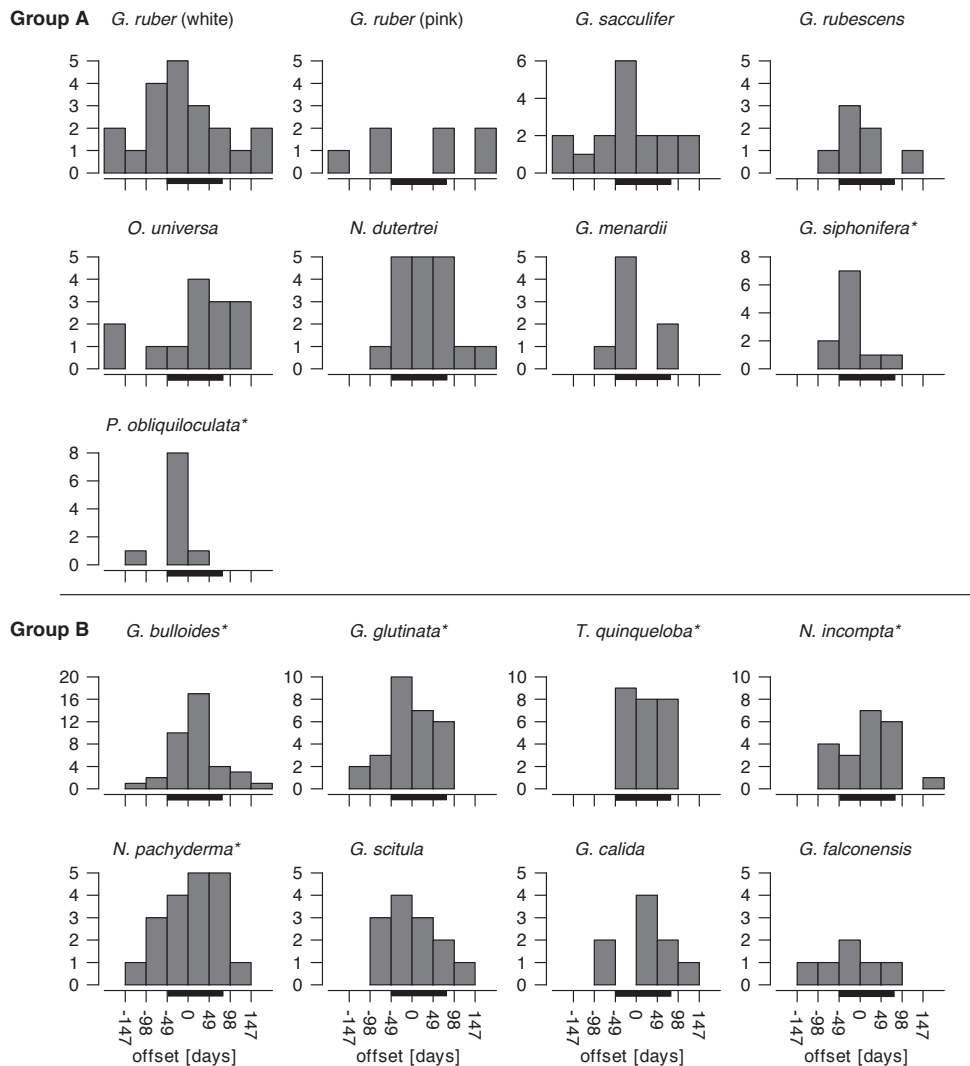
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2 Fig. 6: Scatter plots of proportion of time series with two cycles per year (A) and temperature  
 3 sensitivity of peak prominence (PP') (B) vs. temperature averaged over all sites where a  
 4 species was observed (T<sub>spec</sub>). C and D as A and B, but vs temperature range (ΔT<sub>spec</sub>).  
 5 Individual species are numbered, see table 2.

6



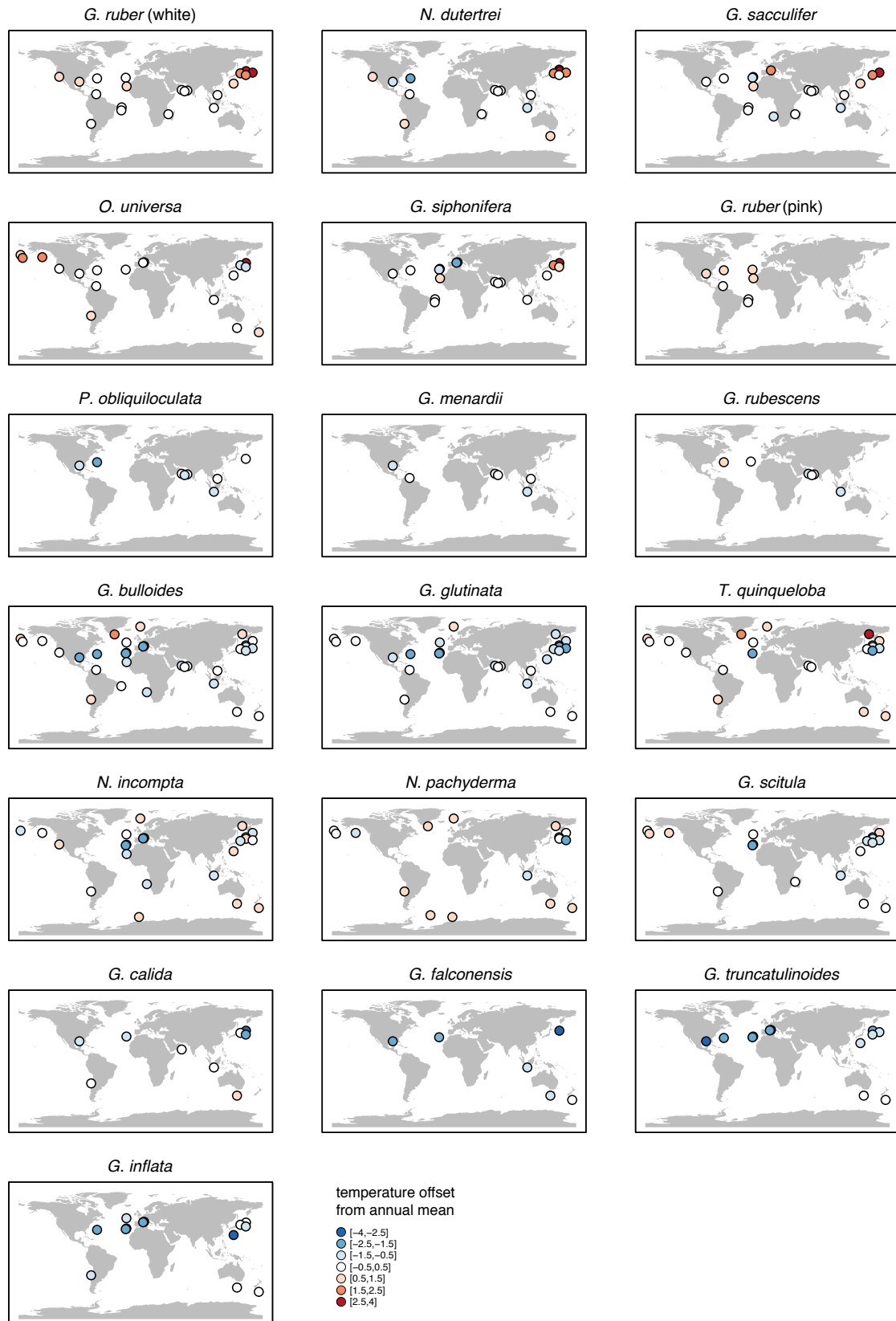
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 2 Fig. 7: As Fig. 5, but peak timing patterns plotted over contour plots of annual temperature  
 3 cycle. See Fig. S8 for other species. Symbols denote ocean basin: squares is Atlantic Ocean,  
 4 circles Indian Ocean and triangles Pacific Ocean. Open symbols indicate site affected by  
 5 upwelling.  
 6



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2 Fig. 8: Productivity and peak timing in groups A and B. Histograms of the residual of  
 3 chlorophyll maxima and peak flux timing. Zero and positive offsets suggest an association  
 4 between shell flux peaks and productivity. The interval used for the binomial test is  
 5 highlighted by the black horizontal bar and species that show a statistically significant  
 6 association ( $p \leq 0.05$ ) between shell flux peak timing and productivity are marked with an  
 7 asterisk.

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2 Fig. 9: offset from mean temperature (0-50 m water depth) due to seasonality. Positive offsets  
 3 indicate that flux-weighted temperature is higher than mean temperature and v.v.