Lunar periodicity in the shell flux of planktonic foraminifera in the Gulf of Mexico

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Abstract. Synchronised reproduction offers clear benefits to planktonic foraminifera – an important group of marine calcifiers – as it increases the chances of successful gamete fusion. Such synchrony requires tuning to an internal or external clock. Evidence exists for lunar reproductive cycles in some species, but its recognition in shell flux time series has proven difficult, raising questions about reproductive strategies. Using spectral analysis of a 4-year time series (mostly at weekly resolution) from the northern Gulf of Mexico, we show that the shell flux of *Globorotalia menardii*, *Globigerinella siphonifera*, *Orbulina universa*, *Globigerinoides sacculifer, Globigerinoides ruber* (both pink and white varieties), *Pulleniatina obliquiloculata*, *Neogloboquadrina dutertrei*, *Globigerinella calida* and *Globigerinita glutinata* is characterised by lunar periodicity. However, the lunar rhythm is not present in all size fractions of each species and tends to be more dominant in the flux of larger shells, consistent with reproduction being more prevalent in larger specimens. Lunar periodicity is superimposed on longer term/seasonal changes in the shell fluxes, but accounts for a significant part of the variance in the fluxes. The amplitude of the lunar cycle increases roughly proportional with the magnitude of the flux, demonstrating that most of the population is indeed affected by lunar-phased synchronisation. In most species peak fluxes occur predominantly around, or just after, full moon. Only *G. siphonifera* and *G. calida* show a contrasting pattern with peaks concentrated around new moon. Although the exact cause of the synchronisation remains elusive, our data considerably increase the number of species for which lunar synchronised reproduction is reported and suggest that such reproductive behaviour is common in many species of planktonic foraminifera.

1 Introduction

Planktonic foraminifera reproduce by releasing large amounts of gametes (Bé et al., 1977; Spindler et al., 1978). However, concentrations of planktonic foraminifera in the open ocean are generally low ($\sim 10^1$ tests m^{-3}) (Berger, 1969; Field, 2004), reducing the chance of gamete fusion. Synchronised reproduction would increase reproductive success and therefore offer great advantage to these free-floating organisms. Reproductive synchrony however, requires the existence of an internal biological clock or an external trigger for reproduction. In their seminal work, Spindler at al. (1979) showed for the first time reproductive synchrony in a planktonic foraminifer. Gamete release in *Hastigerina pelagica* in laboratory culture occurs with lunar periodicity approximately 5 days after each full moon (Spindler et al., 1979). Synchronised gamete release was however not observed in other species kept in the same laboratories (Hemleben et al., 1989). Yet, lunar and semi-lunar periodicity was subsequently observed in nature in the abundance and test size of several species. The first indications stem from the Red Sea (Almogi-Labin, 1984) and are based on repeated plankton tows at a single location. Bijma et al. (1990) inferred a lunar reproductive cycle in *Globigerinoides sacculifer* (confirmed by Erez et al., 1991) and semi-lunar cycles in *Globigerinoides ruber* and *Globigerinella siphonifera*. Lunar reproduction is also suggested for *Globigerina bulloides* (Schiebel

et al., 1997) and for *Neogloboquadrina pachyderma* (Volkmann, 2000), but these studies involved sampling at different locations and aliasing due to patchiness and/or interference with the lunar cycle as a result of sampling across physical or ecological gradients cannot be excluded (Lončarić et al., 2005).

The existence of lunar periodicity in the export flux of planktonic foraminiferal tests is even less constrained, in part due to a lack of sufficiently high-resolved time series of shell fluxes. Data from the Pacific Ocean (Kawahata et al., 2002) hint at the intermittent presence of a lunar cycle in the fluxes of *G. sacculifer*, *G. ruber*, *Orbulina universa* and *G. siphonifera*, but the resolution of these observations is too low to draw firm conclusions. The only species for which lunar periodicity in the shell flux has been convincingly demonstrated is *H. pelagica* (Lončarić et al., 2005). However, these authors found no indications for lunar cycles in the shell flux of any other species present at the sediment trap site in the south-east Atlantic Ocean.

Whilst important for the understanding of reproductive strategies of planktonic foraminifera, it remains unresolved if lunar periodicity stems from endogenous or exogenous forcing. In addition, whether or not lunar periodicity in the export flux (and hence a potential effect on the sedimentary record) is restricted to *H. pelagica* remains equivocal. As discussed above, the few data currently available suggest that the expression of lunar periods in foraminifera may be temporally and/or spatially variable. As such, more and longer high-resolution time series are needed to answer these questions. Here we investigate a 4-year time series of shell fluxes from the northern Gulf of Mexico. Seasonal flux patterns at this location have been described elsewhere (Poore et al., 2013) and in this study we focus exclusively on higher frequency variability.

2 Hydrographic setting

Surface hydrography in the Gulf of Mexico exhibits large seasonal variations in temperature and salinity. Summer sea surface temperatures exceed 30 °C with a surface mixed-layer depth between 30 and 50 m, while winter sea surface temperature minima fall below 20 °C, with a mixed layer depth of ∼ 100 m (Poore et al., 2013). Average sea surface salinity varies by > 2 units around 35.5, with lower values in summer and higher values in winter (Poore et al., 2013). The site primarily reflects open Gulf of Mexico conditions. Nevertheless, anomalously high Mississippi discharge events may lead to short-term salinity reductions in the surface layer. For example, a low salinity lens was observed in the upper 10 m of the water column in July 2008, but this did not affect the shell fluxes of planktonic foraminifera (Poore et al., 2013). In addition, aperiodic westward propagation of loop current or warm-core eddies in the Gulf of Mexico can occasionally bring anomalously oligotrophic, warm and salty

water to the study site (Vukovich, 2007; Vukovich and Maul, 1985).

3 Material and methods

We analyse previously published (2010–2012; Reynolds et al., 2013) and unpublished (2012–2014) shell flux data from a sediment trap time series from the northern Gulf of Mexico (27.5° N, 90.3° W; 700 m water depth; 400 m above the sea floor) spanning four years, mostly at weekly resolution. Full methods on the sediment trap mooring and foraminifera analysis are described in Poore et al. (2013) and Reynolds et al. (2013). Shell fluxes are separated in six sieve-size fractions (150–212, 212–300, 300–425, 425–500, 500–600 and > 600 μm).

The average sampling resolution of the time series is ∼ 9 days, which is more than sufficient to resolve lunar cyclicity (period 29.5 days), but insufficient to resolve semi-lunar cycles. Each size-specific time series was analysed by the mid-date of the collection interval. Prior to analysis, linear trends in the data were removed and all fluxes were normalised to unit variance. Spectral analysis was performed in R using REDFIT (Bunn, 2008; R core team, 2014; Schulz and Mudelsee, 2002), which uses a first-order autoregressive (AR1) process to account for memory effects associated with autocorrelation in the time series to estimate spectral peak significance. To estimate the temporal patterns of spectral power in the lunar frequency band, continuous Morlet wavelet transform was performed on linearly interpolated data (7-day resolution) using the dplR package (Bunn, 2008; Rioul and Vetterli, 1991).

Data from *Globorotalia truncatulinoides*, *G. bulloides* and *Globigerina falconensis* were not analysed since these species show only very brief pulses of high shell flux in winter, precluding meaningful spectral analysis. Such intermittency of the flux was also the case for some size classes, particularly the largest and smallest, in several species. These cases have not been analysed and are indicated in Table 1.

4 Results

All species show (quasi-)seasonal variations in the shell flux (Fig. 1). Superimposed on the seasonal cycle, many species show higher frequency variability and lunar periodicity is readily apparent in several species (Fig. 1). This is clearest in the shell flux of *Globorotalia menardii*, which peaks around full moon and *G. siphonifera*, which seems to peak preferentially around new moon (Fig. 1). Spectral analysis supports these observations and reveals statistically significant power at, or very close to, the lunar frequency in one or more size fractions of all species except *Globorotalia crassaformis* (Table 1, Supplement Fig. S1).

In the following we show figures for *G. siphonifera* as an example and summarise results for the remaining species

Table 1. Lunar periodicity in the shell flux of planktonic foraminifera in the Gulf of Mexico. Y/N: presence, absence of significant spectral power at lunar frequency at 95 % confidence interval (bold: 99 % confidence); na: not analysed because of intermittency of the shell flux.

	> 600 µm	500–600 µm	425–500 µm	300–425 µm	212–300 µm	150–212 µm
G. menardii	Y	**Y**	**Y**	**Y**	**Y**	**Y**
G. siphonifera	**Y**	**Y**	**Y**	N	N	N
O. universa	N	Y	Y	N	na	na
G. sacculifer	N	N	N	**Y**	Y	N
G. ruber (pink)	na	N	Y	**Y**	N	N
G. ruber (white)	na	na	N	N	Y	Y
P. obliquiloculata	na	N	Y	**Y**	N	N
N. dutertrei	na	na	N	**Y**	Y	N
G. calida	na	na	Y	N	N	N
G. crassaformis	na	na	N	N	N	N
G. glutinata	na	na	na	na	N	Y

Table 2. Phasing of lunar cycles in shell fluxes. Phasing determined from counting the number of peaks above 10 % of the maximum flux per lunar week; see also Figs. 4 and S3. 1: new moon; 2: first quarter; 3: full moon; 4: third quarter. Empty cells indicate cases where no statistically significant lunar periodicity could be detected.

	> 600 µm	500–600 µm	425–500 µm	300–425 µm	212–300 µm	150–212 µm
G. menardii	3, 4	3	3, 4	4	3	3
G. siphonifera	1	1	1			
O. universa		3	4			
G. sacculifer				3, 4	4	
G. ruber (pink)			3, 4	3, 4		
G. ruber (white)					2–4	4
P. obliquiloculata			3,4	3, 4		
N. dutertrei				3	4	
G. calida			1, 2			
G. glutinata						4

in Tables 1 and 2 (associated figures for all species can be found in the supplement). The patterns are most pronounced in *G. menardii* and *G. siphonifera,* which show significant spectral power at the lunar frequency with 99 % confidence in more than two size fractions. In *G. siphonifera* only the three largest size fractions show significant peaks in spectral power at the lunar frequency (Fig. 2). This pattern of lunar periodicity being present predominantly in the flux of larger shells can also be seen in most other species, although often the flux of the largest shells is too low and intermittent to statistically assess periodicity within this size class (Fig. S1). In *G. siphonifera* and *G. menardii* the spectral peaks at the lunar frequency are often higher than those at both annual and semi-annual frequencies, indicating that compared to variance at the lunar timescale, seasonal variance is very small (Figs. 2, S1). Although in other species the peaks at annual and semi-annual frequencies are often larger, flux variability at lunar frequencies appears to explain a non-negligible proportion of the total variance in the flux time series (Fig. S1). This clearly highlights the importance of lunar periodicity on shell flux variability.

It is also evident from the raw flux data (Fig. 1) that the persistence and amplitude of the lunar frequency variability in the shell fluxes is not stationary, but varies over time. Clearly, lunar periodicity can only express itself when shell fluxes are above zero, but there also seems to be some modulation of the amplitude of the lunar cycle in the shell fluxes, with larger amplitude variability when the overall fluxes are higher (Fig. 1). The continuous wavelet transform of the shell flux data indeed shows clear variation in the power at the lunar frequency (Fig. 3 for *G. siphonifera*; S2 for all other species), which seems approximately proportional to the magnitude of the flux. This analysis also hints at the intermittent presence of lunar periodicity in the flux *G. crassaformis* (Fig. S2).

In most species peaks in the shell flux dominantly occur around, or in the week following, full moon (Table 2; Fig. S3). *G. siphonifera* and *Globigerinella calida* are the only species that show peaks mostly in the week around new moon (Fig. 4). In *O. universa*, *G. sacculifer* and *Neogloboquadrina dutertrei* there seems to be a trend towards flux peaks occurring later in smaller size classes, which could be
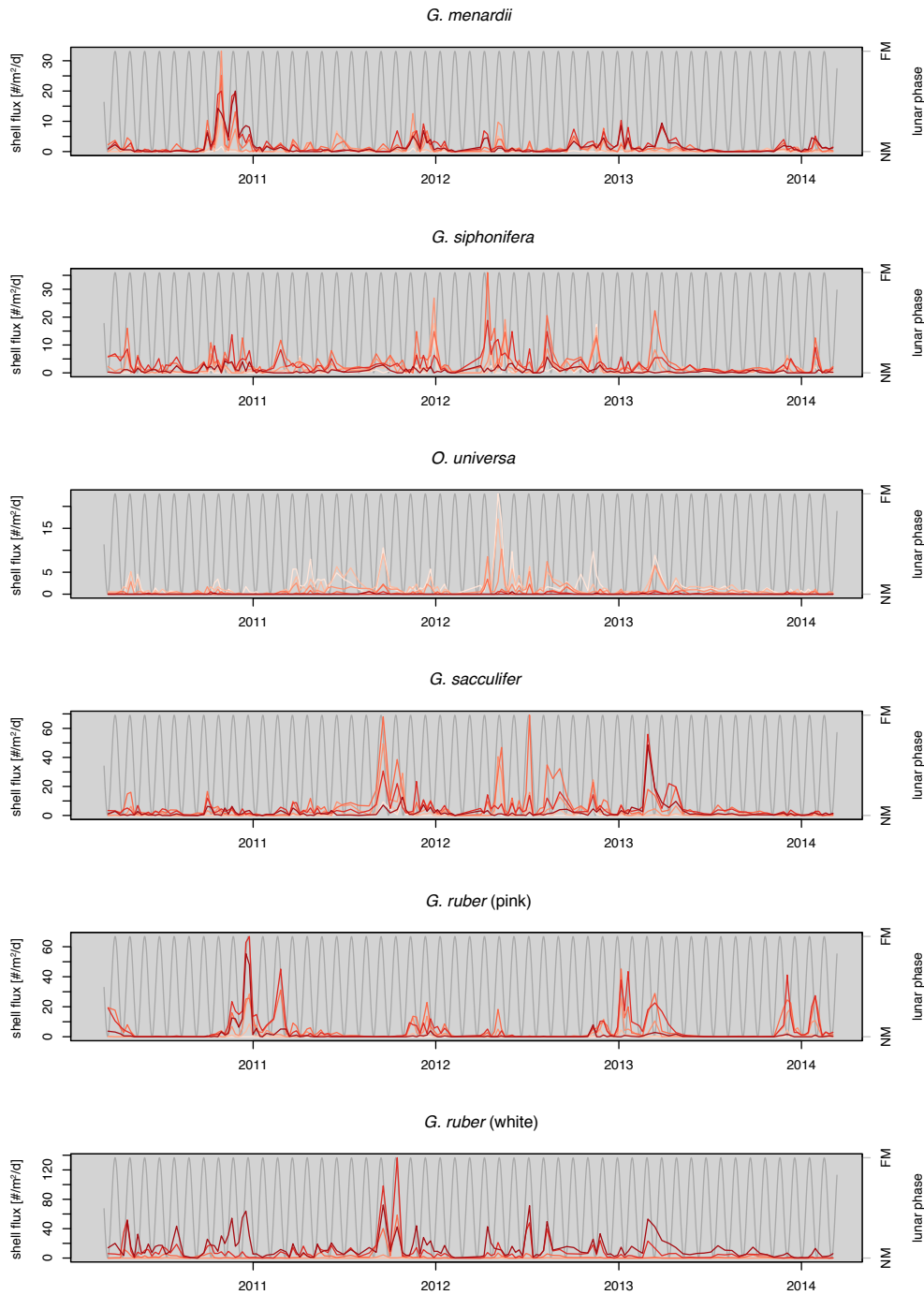
Figure 1.

related to a slower sinking speed of smaller tests, but such a trend is not apparent in other species.

5 Discussion

The shell fluxes of 11 species in the time series from the northern Gulf of Mexico showed some degree of lunar pe-

riodicity. The different phasing among the species (Fig. S3) and the different temporal evolution of variance in the lunar frequency band (Fig. S2) indicate that this periodicity is not due to tidally synchronised lateral advection of shells, but instead reflects a primary signal in the shell flux, most likely related to the reproductive cycle. The tendency for lunar periodicity to be more present in larger shells also supports that the periodicity reflects reproductive synchronisation, since
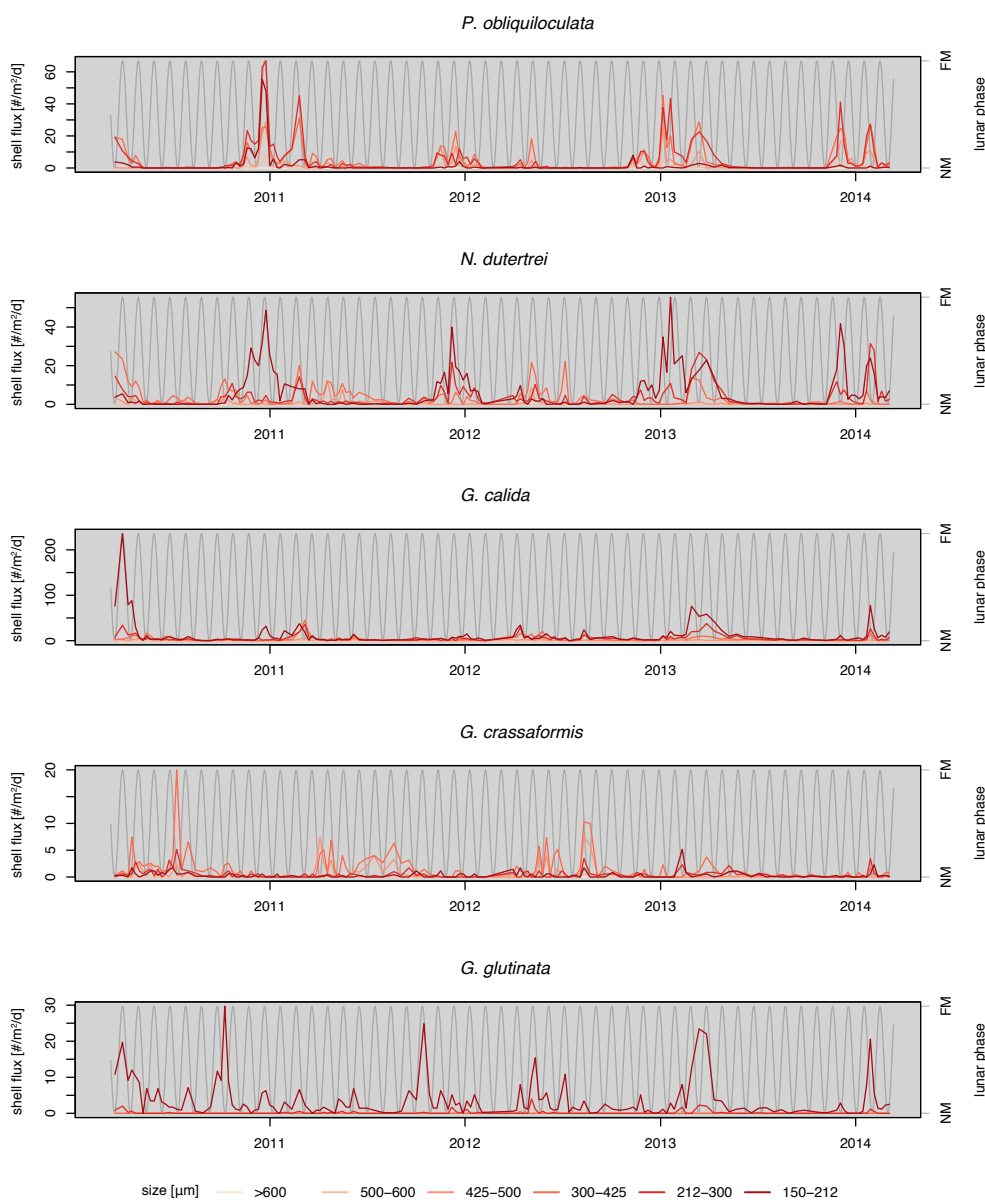
Figure 1. Planktonic foraminifera shell flux time series separated by size fraction from the northern Gulf of Mexico. Grey curve in the background represents the lunar cycle; NM: new moon; FM: full moon. Lunar periodicity, superimposed on a seasonal cycle, is readily visible in the flux of *G. menardii* and *G. siphonifera*.

it has previously been shown that the proportion of specimens that have undergone gametogenesis increases with size (Bé et al., 1981; Bijma and Hemleben, 1994). Moreover, the presence of sac-bearing *G. sacculifer*, which must have undergone gametogenesis (Hemleben et al., 1989), in the fine fraction of this species further corroborates the reproductive nature of the lunar periodicity in the shell fluxes.

This lunar cyclicity suggests a life span of approximately one lunar cycle (Bijma et al., 1990; Hemleben et al., 1989; Spindler et al., 1979). Nevertheless, some species have in the laboratory been observed to be able to skip a cycle and reproduce around the following full moon (Spindler et al., 1979) and field evidence also suggests that a non-calcifying population may survive for several months under unfavourable conditions (Jonkers et al., 2010). The magnitude or amplitude of the lunar cycle in the shell fluxes varies temporally (Figs. 1, 3 and S2). To a first order the expression of lunar periodicity is related to the magnitude of the shell flux (Figs. 3, S2), illustrating that almost the entire population
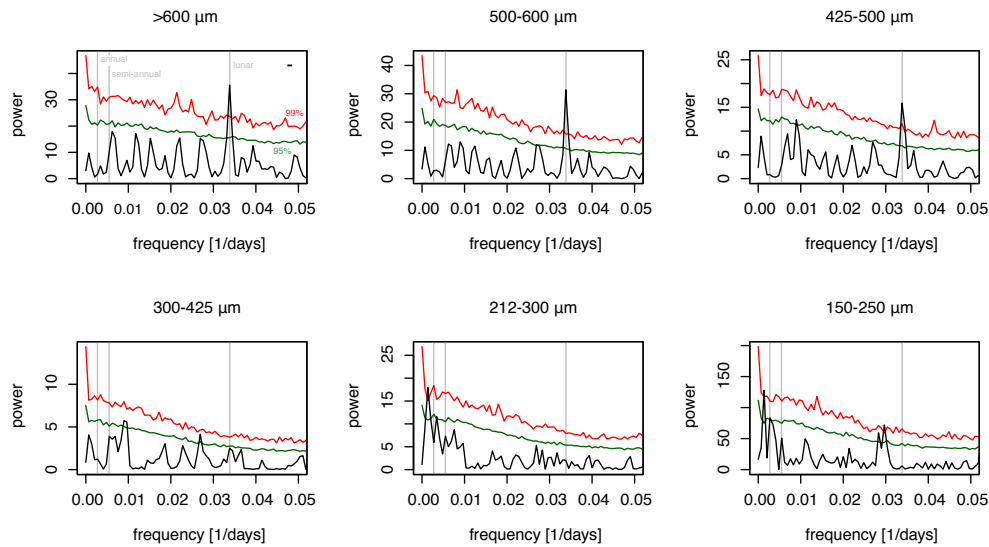
Figure 2. Periodograms of the size-fractionated shell flux time series of *G. siphonifera* (for other species see Fig. S1). Vertical grey bars denote annual and lunar frequencies. The horizontal black line in the upper left panel indicates the 6 dB bandwidth. Red and green lines show 99 and 95 % confidence limits. Lunar periodicity is clearly present in the three largest size fractions.
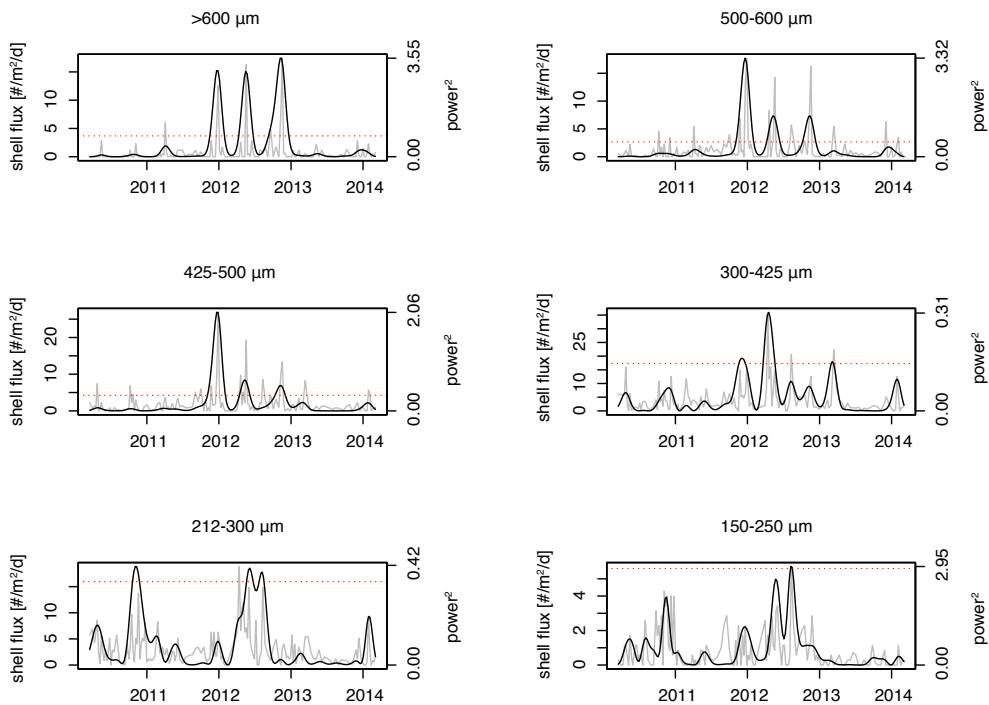

Figure 3. Temporal expression of lunar periodicity in shell flux of *G. siphonifera* (for other species see Fig. S2). Raw shell flux (grey) overlain with the squared spectral power at the lunar frequency (estimated using continuous Morlet wave transformation, see material and methods; black). The red dashed line represents the 90 % confidence interval. Lunar periodicity tends to be more expressed (have higher power) when fluxes are higher.

is affected by the lunar cycle, in line with a dominant life span of approximately 1 month. There are also periods when shell fluxes are above background when the lunar periodicity has no, or only little, power, perhaps due to other drivers or

random variability in the export flux and a reduced signal to noise ratio (Fig. S2). Importantly, such temporal variability has not been observed previously and clearly demonstrates the need for long (multi-year) high-resolution shell flux time
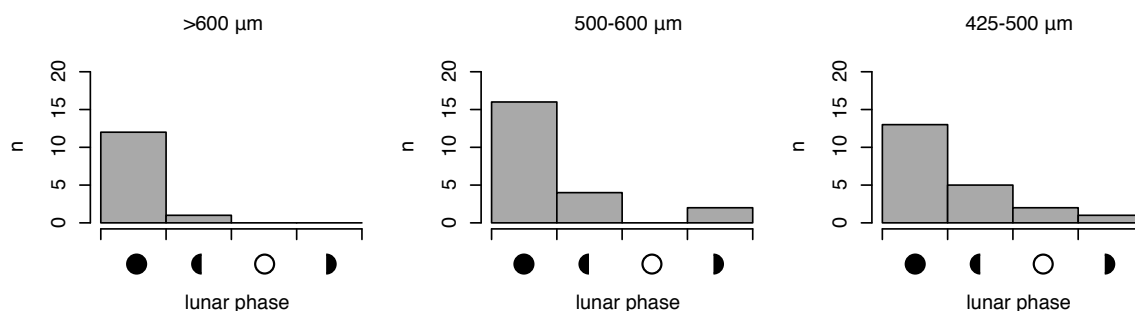
Figure 4. Phasing of the lunar cycle in shell fluxes of *G. siphonifera* (for other species see Fig. S3). Histograms of the number of peaks above 10 % of the maximum flux per lunar phase for size fractions where lunar periodicity is statistically significant.

series to further understand the influence of lunar periodicity on the export of planktonic foraminiferal shell across a range of oceanographic settings.

The potential importance of lunar cyclicity in the fossil record ultimately depends on the relative importance of the lunar versus long-term/seasonal cycle. In some species – and in some size fractions – the ratio of spectral power in the lunar and seasonal frequency is close to, or greater than, one (e.g. *G. siphonifera* and *G. menardii*; Figs. 2 and S1); this highlights the importance of lunar cyclicity in shell flux variance in these species. In most other species, however, there is more spectral power in the seasonal band. Together with the covariability between shell flux and lunar cycle amplitude, this demonstrates the importance of the long-term/seasonal cycles in the shell flux for the fossil signal of planktonic foraminifera (cf. Jonkers and Kučera, 2015).

Our observations are in agreement with earlier studies in the Red Sea (Bijma et al., 1990; Erez et al., 1991) and corroborate the low-resolution observations from the Pacific Ocean (Kawahata et al., 2002). Bijma et al. (1990) suggested a semi-lunar cycle for *G. ruber* and *G. siphonifera*. The resolution of our time series is, however, insufficient to test for the presence of such periodicity and we cannot rule out nor confirm these observations. Importantly however, in the Gulf of Mexico sediment trap times series all 11, including non-spinose, species show lunar periodicity in at least one size fraction. The scarcity of significant spectral power at the lunar frequency in small-sized foraminifera is in agreement with a high mortality amongst these specimens (Bijma and Hemleben, 1994). Occasional absence in larger specimens also probably reflects failure to detect the lunar signal due to low and intermittent fluxes. In fact, occasional pairing of flux peaks may hint that synchronised flux variability and lunar periodicity could be present, in these size fractions, but poorly and only sporadically expressed. Regardless, our observations of a periodic lunar component in (part of) the flux of all species suggests that lunar synchronised reproduction is ubiquitous, rather than the exception in planktonic foraminifera.

Lunar periodicity in foraminiferal shell fluxes was, up to now, only demonstrated for *H. pelagica* from a single site in the south-east Atlantic Ocean (Lončarić et al., 2005). Despite the high resolution of this study, Lončarić et al. (2005) did not observe lunar periodicity in the shell flux of other species and suggested that lunar synchronised reproduction was unique to *H. pelagica*. Our data suggest otherwise and we offer two potential reasons why lunar periodicity was not observed in the south-east Atlantic: (i) temporally variable prominence of lunar periodicity and (ii) obscuration by non-periodic flux variability in certain size fractions. Indeed, significant lunar cyclicity in the Gulf of Mexico time series could in several species only be detected when the size-fractionated data were analysed. Further potential complications in detecting lunar periodicity in the shell flux of planktonic foraminifera could relate to the inherent nature of sediment traps that cannot easily account for differential settling velocity and the consequent smearing of the shell fluxes (Takahashi and Bé, 1984), nor for lateral advection of shells over long distances (Von Gyldenfeldt et al., 2000).

To assess the phasing of the peaks in the shell flux and of reproduction with respect to the lunar cycle, the settling time and life cycle of planktonic foraminifera needs to be taken into account. Sinking speeds of foraminiferal shells vary by an order of magnitude, but are generally between 200 and 500 m day^{-1} (Takahashi and Bé, 1984). This means that shells most likely arrive within 3 days after death at the sediment trap at 700 m depth. For specimens that died after gametogenesis this delay is probably even smaller, since several species descend (up to) hundreds of metres in the water column before reproduction (Erez et al., 1991; Hemleben et al., 1989). Because this estimate of settling delay is within the average collecting interval of the sediment traps we do not apply a correction for settling. Furthermore, the time between gametogenesis and death (start of sinking) is most likely very short and insignificant with respect to the average duration of the collecting intervals. Thus, shells that completed their life cycle arrive at the sediment trap shortly after reproduction.

The phasing of the flux is similar for most species, with peaks in the shell flux predominantly occurring around or in the week following full moon. Only *G. siphonifera* and *G. calida* flux peaks predominantly occur around new moon (Table 2; Fig. S3). For some size fractions the number of peaks is low, potentially affecting the estimates of phasing with respect to the lunar cycle, but the general agreement among the timing of the different size fractions indicates that our estimates are robust. Previously, lunar (and semi-lunar) reproductive cycles in *G. siphonifera*, *G. ruber* and *G. sacculifer* were inferred from abundance and size variations (Bijma et al., 1990; Erez et al., 1991). Maxima in the abundance of these species were found to occur 9 to 3 days before full moon, followed by reproduction around full moon (Bijma et al., 1990; Erez et al., 1991). This clearly shows the temporal decoupling between abundance, reproduction and death (i.e. export flux). In the Gulf of Mexico *G. ruber* (pink and white) and *G. sacculifer* show a phasing broadly in agreement with the observations in the Red Sea, although a non-negligible part of the flux peaks appears to occur in the week following full moon (Table 2). Bijma et al. (1990) also mention in passing that spherical *O. universa* are most abundant in surface waters off Bermuda and Curaçao around full moon, suggesting a lunar cycle for this species that is in phase with full moon. The maximum in peak occurrence around the same time in the Gulf of Mexico would be consistent with these observations.

The phasing of peaks in *G. siphonifera* and *G. calida* is unique among the species analysed here, and in the case of *G. siphonifera*, clearly different from that reported by Bijma et al. (1990). Although the delay due to settling may vary among species, such differences are unlikely to explain contrasting in phasing of *G. siphonifera* and *G. calida*. The difference is therefore probably real and such a temporal separation of reproduction among species may indeed add to the reproductive success as it is likely to increase the chances of gamete fusion within the same species. Alternatively, Bijma et al. (1994) argued that the phasing of flux peaks is a function of reproduction level, where changes in the reproduction level could shift the peak flux from new to full moon.

Whilst the advantage of synchronised reproduction for planktonic foraminfera is obvious, the actual mechanism ensuring lunar synchrony is unclear. In many marine organisms lunar reproduction is thought to be endogenous and possibly phase-locked by an external Zeitgeber (see reviews by Naylor, 2010 and references therein; Neumann, 2014). However, because the reproductive rhythm of *H. pelagica* could be modulated (unpublished results from Hemleben and Spindler, mentioned in Bijma et al., 1990) and (semi-)lunar periodicity in other species was never observed in laboratory conditions, Bijma et al. (1990) argued that in planktonic foraminifera lunar reproduction is caused by an unknown exogenous trigger. Spatial variability in the presence of lunar synchronised reproduction, as suggested by the absence of a lunar rhythm in the shell flux in the south-east Atlantic

(Lončarić et al., 2005) in species that show such a rhythm in the Gulf of Mexico, would be in line with such an exogenous mechanism. However, as discussed above, there might be several reasons why lunar periodicity was not detected in the south-east Atlantic time series.

Culture studies have shown that reproduction in planktonic foraminifera can be modulated by light and food availability (Bé et al., 1981; Caron et al., 1982), making (changes in) these parameters potential triggers, or environmental cues, for reproduction. If foraminifera had an internal counting mechanism, diurnal light–dark cycles could be a cue for reproduction, albeit an ambiguous one that is sensitive to cloudiness and depth habitat. If food availability were the trigger for reproduction, one would expect lunar periodicity in food availability. While we cannot assess whether or not such a cycle is present in zooplankton abundance, there is no indication that phytoplankton abundance shows such a rhythm (based on spectral analysis of chlorophyll *a* concentration, not shown).

In the Gulf of Mexico, time series lunar shell flux periodicity is expressed at different times during the year (Fig. S2), suggesting that an exogenous trigger or a Zeitgeber is continuously present and not dependent on seasonal variability. The predominance of reproduction occurring around full moon also suggests that most species respond to the same trigger. However, our data set does not allow establishing the exact mechanism responsible for the observed lunar cyclicity. Clearly, more studies, both in the field and in the laboratory, are needed to elucidate the cause of (semi-)lunar reproductive synchrony in planktonic foraminifera.

Regardless of the exact mechanism, our observations provide strong evidence that synchronised reproduction is common in planktonic foraminifera. Besides having clear benefits for their reproductive success, the lunar periodicity in the shell flux may also affect short-term variability in the total particulate flux from the surface ocean. Planktonic foraminifera are major contributors to the global carbonate flux to the deep ocean (Schiebel, 2002) and lunar cyclicity could therefore influence variability of this flux. Little is known about the ballasting potential of foraminifera, but most studies indicate that it is fairly low due to their fast sinking speeds (e.g. Fischer and Karakaş, 2009; Schmidt et al., 2014). A direct effect of lunar periodicity on short-term variability of the biological pump is therefore unlikely. However, lunar synchronised reproduction of foraminifera potentially influences the ratio of (particulate) inorganic/organic carbon in the surface ocean and of the total export flux and could in that way contribute to variability in the strength of the biological pump.

6 Conclusions

High-resolution shell flux time series of planktonic foraminifera from the northern Gulf of Mexico reveal lunar periodicity in *G. menardii*, *G. siphonifera*, *O. universa*, *G. sacculifer*, *G. ruber* (pink and white), *P. obliquiloculata*, *N. dutertrei*, *G. calida*, *G. crassaformis* and *G. glutinata*. However, such periodicity could not be detected in all size fractions and, in many species, tends to be more prevalent in larger shells, consistent with the notion that reproduction occurs more frequently in large (adult) specimens.

In almost all species peaks in the shell flux occur around full moon and/or in the week following full moon, suggesting that reproduction occurs in response to the same trigger. Only *G. siphonifera* and *G. calida* show an opposite pattern, with most shell flux peaks occurring around new moon. In some species (e.g. *G. siphonifera* and *G. menardii*) the amplitude of lunar flux variability is larger than, or equals the seasonal flux variability, clearly demonstrating the importance of a lunar rhythm in determining export flux variability. However, in all species lunar periodicity is superimposed on longer term/seasonal variability in the shell flux and hence is not continuously expressed in the sediment trap time series. Consequently, the seasonal cycle dominates variability in the magnitude of the export flux in most species.

While the exact mechanism, be it exogenous or endogenous, for lunar periodicity in the shell flux remains unknown, our analysis reveals for the first time that lunar synchronised reproduction is a feature of many species of planktonic foraminifera.

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