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

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11 Abstract

12 Synchronised reproduction offers clear benefits to planktonic foraminifera - an important

13 group of marine calcifiers - as it increases the chances of successful gamete fusion. Such

14 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

17 time series (mostly at weekly resolution) from the northern Gulf of Mexico we show that the

18 shell flux of *Globorotalia menardii*, *Globigerinella siphonifera*, *Orbulina universa*,

19 *Globigerinoides sacculifer, Globigerinoides ruber* (both pink and white varieties),

20 Pulleniatina obliquiloculata, Neogloboquadrina dutertrei, Globigerinella calida and

21 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

24 periodicity is superimposed on longer term/seasonal changes in the shell fluxes, but accounts

25 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

27 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

1 the synchronisation remains elusive, our data considerably increase the number of species for

2 which lunar synchronised reproduction is reported and suggest that such reproductive

3 behaviour is common in many species of planktonic foraminifera.

4

5 1 Introduction

Planktonic foraminifera reproduce by releasing large amounts of gametes (Bé et al., 1977; 6 Spindler et al., 1978). However, concentrations of planktonic foraminifera in the open ocean 7 are generally low ($\sim 10^1$ tests m⁻³) (Berger, 1969; Field, 2004) reducing the chance gamete 8 fusion. Synchronised reproduction would increase reproductive success and therefore offer 9 great advantage to these free-floating organisms. Reproductive synchrony however, requires 10 the existence of an internal biological clock or an external trigger for reproduction. In their 11 seminal work, Spindler at al. (1979) showed for the first time reproductive synchrony in a 12 planktonic foraminifer. Gamete release in *Hastigerina pelagica* in laboratory culture occurs 13 with lunar periodicity approximately five days after each full moon (Spindler et al., 1979). 14 Synchronised gamete release was however not observed in other species kept in the same 15 laboratories (Hemleben et al., 1989). Yet, lunar and semi-lunar periodicity was subsequently 16 observed in nature in the abundance and test size of several species. The first indications stem 17 from the Red Sea (Almogi-Labin, 1984) and are based on repeated plankton tows at a single 18 location Bijma et al. (1990) inferred a lunar reproductive cycle in *Globigerinoides sacculifer* 19 (confirmed by Erez et al., (1991)) and semi-lunar cycles in Globigerinoides ruber and 20 Globigerinella siphonifera. Lunar reproduction is also suggested for Globigerina bulloides 21 (Schiebel et al., 1997) and for Neogloboquadrina pachyderma (Volkmann, 2000), but these 22 studies involved sampling at different locations and aliasing due to patchiness and/or 23 interference with the lunar cycle as a result of sampling across physical or ecological 24 gradients cannot be excluded (Lončarić et al., 2005). 25

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) hints 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

31 which lunar periodicity in the shell flux has been convincingly demonstrated is *H. pelagica*

32 (Lončarić et al., 2005). However, these authors found no indications for lunar cycles in the

1 shell flux of any other species present at the sediment trap site in the southeast Atlantic

2 Ocean.

Whilst important for the understanding of reproductive strategies of planktonic foraminifera, 3 it remains unresolved if lunar periodicity stems from endogenous or exogenous forcing. In 4 addition, whether or not lunar periodicity in the export flux (and hence a potential effect on 5 the sedimentary record) is restricted to *H. pelagica* remains equivocal. As discussed above, 6 the few data currently available suggest that the expression of lunar periods in foraminifera 7 may be temporally and/or spatially variable. As such, more and longer high-resolution time 8 series are needed to answer these questions. Here we investigate a 4-year time series of shell 9 fluxes from the northern Gulf of Mexico. Seasonal flux patterns at this location have been 10 described elsewhere (Poore et al., 2013) and in this study we focus exclusively on higher 11 frequency variability... 12

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14 2 Hydrographic setting

Surface hydrography in the Gulf of Mexico exhibits large seasonal variations in temperature 15 and salinity. Summer sea surface temperatures exceed 30 °C with a surface mixed layer depth 16 between 30 and 50 meters, while winter sea surface temperature minima fall below 20 °C, 17 with a mixed layer depth of ~100 meters (Poore et al., 2013). Average sea surface salinity 18 varies over by >2 units around 35.5, with lower values in summer and higher values in winter 19 (Poore et al., 2013). The site primarily reflects open Gulf of Mexico conditions. Nevertheless, 20 anomalously high Mississippi discharge events may lead to short-term salinity reductions in 21 the surface layer. For example, a low salinity lens was observed in the upper 10 m of the 22 water column in July 2008, but this did not affect the shell fluxes of planktonic foraminifera 23 (Poore et al., 2013). In addition, aperiodic westward propagation of loop current or warm-core 24 eddies in the Gulf of Mexico can occasionally bring anomalously oligotrophic, warm and 25 salty water to the study site (Vukovich, 2007; Vukovich and Maul, 1985). 26

27

28 3 Material and methods

29 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

31 (27.5° N, 90.3° W, 700 m water depth, 400 m above the sea floor) spanning 4 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 μ m, 212-300 μ m, 300-425 μ m, 425-500 μ m, 500-600 μ m and >600 μ m).

The average sampling resolution of the time series is ~ 9 days, which is more than sufficient to 5 resolve lunar cyclicity (period 29.5 days), but insufficient to resolve semi-lunar cycles. Each 6 size-specific time series was analysed by the mid date of the collection interval. Prior to 7 analysis linear trends in the data were removed and all fluxes were normalised to unit 8 variance. Spectral analysis was performed in R using REDFIT (Bunn, 2008; R core team, 9 2013; Schulz and Mudelsee, 2002), which uses a first-order autoregressive (AR1) process to 10 account for memory effects associated with autocorrelation in the a time series to estimate 11 spectral peak significance. To estimate the temporal patterns of spectral power in the lunar 12 frequency band, continuous Morlet wavelet transform was performed on linearly interpolated 13 data (7 day resolution) using the dplR package (Bunn, 2008; Rioul and Vetterli, 1991). 14 Data from Globorotalia truncatulinoides, G. bulloides and Globigerina falconensis were not 15

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.

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21 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

27 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, Fig. S1).

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

the remaining species in tables 1 and 2 (associated figures for all species can be found in the

supplement to this paper). The patterns are most pronounced in *G. menardii* and *G.*

siphonifera, which show significant spectral power at the lunar frequency with 99 % 1 confidence in more than two size fractions. In G. siphonifera only the three largest size 2 fractions show significant peaks in spectral power at the lunar frequency (Fig. 2). This pattern 3 of lunar periodicity being present predominantly in the flux of larger shells can also be seen in 4 5 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. 6 *menardii* the spectral peaks at the lunar frequency are often higher than those at both annual 7 and semi-annual frequencies, indicating that compared to variance at the lunar time scale, 8 seasonal variance is very small (Fig. 2, S1). Although in other species the peaks at annual and 9 semi-annual frequencies are often larger, flux variability at lunar frequencies appears to 10 explain a non-negligible proportion of the total variance in the flux time series (Fig. S1). This 11 clearly highlights the importance of lunar periodicity on shell flux variability. 12

It is also evident from the raw flux data (Fig. 1) that the persistence and amplitude of the lunar 13 frequency variability in the shell fluxes is not stationary, but varies over time. Clearly, lunar 14 periodicity can only express itself when shell fluxes are above zero, but there also seems to be 15 some modulation of the amplitude of the lunar cycle in the shell fluxes, with larger amplitude 16 variability when the overall fluxes are higher (Fig. 1). The continuous wavelet transform of 17 the shell flux data indeed shows clear variation in the power at the lunar frequency (Fig. 3 for 18 G. siphonifera; S2 for all other species), which seems approximately proportional to the 19 magnitude of the flux. This analysis also hints at the intermittent presence of lunar periodicity 20 in the flux G. crassaformis (Fig. S2). 21

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

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29 5 Discussion

The shell fluxes of 11 species in the time series from the northern Gulf of Mexico showed some degree of lunar periodicity. 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 1 reflects a primary signal in the shell flux, most likely related to the reproductive cycle. The 2 tendency for lunar periodicity to be more present in larger shells also supports that the 3 periodicity reflects reproductive synchronisation, since it has previously been shown that the 4 5 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, 6 which must have undergone gametogenesis (Hemleben et al., 1989), in the fine fraction of 7 this species further corroborates the reproductive nature of the lunar periodicity in the shell 8 fluxes. 9

This lunar cyclicity suggests a life span of approximately one lunar cycle (Bijma et al., 1990; 10 Hemleben et al., 1989; Spindler et al., 1979). Nevertheless some species have in the 11 laboratory been observed to be able to skip a cycle and reproduce around the following full 12 moon (Spindler et al., 1979) and field evidence also suggests that a non-calcifying population 13 may survive for several months under unfavourable conditions (Jonkers et al., 2010). The 14 magnitude or amplitude of the lunar cycle in the shell fluxes varies temporally (Fig. 1, 3 and 15 S2). To a first order the expression of lunar periodicity is related to the magnitude of the shell 16 flux (Fig. 3, S2), illustrating that almost the entire population is affected by the lunar cycle, in 17 line with a dominant life span of approximately one month. There are also periods when shell 18 fluxes are above background when the lunar periodicity has no, or only little, power, perhaps 19 due to other drivers or random variability in the export flux and a reduced signal to noise 20 ratios (Fig. S2). Importantly, such temporal variability has not been observed previously and 21 clearly demonstrates the need for long (multi-year) high-resolution shell flux time series to 22 further understand the influence of lunar periodicity on the export of planktonic foraminiferal 23 shell across a range of oceanographic settings. 24

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*; Fig. 2 and S1) highlighting 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 long1 term/seasonal cycles in the shell flux for the fossil signal of planktonic foraminifera (cf.

2 Jonkers and Kučera, 2015).

Our observations are in agreement with earlier studies in the Red Sea (Bijma et al., 1990; Erez 3 et al., 1991) and corroborate the low-resolution observations from the Pacific Ocean 4 (Kawahata et al., 2002). Bijma et al. (1990) suggested a semi-lunar cycle for Globigerinoides 5 ruber and G. siphonifera. The resolution of our time series is however insufficient to test for 6 the presence of such periodicity and we cannot rule out nor confirm these observations. 7 Importantly however, in the Gulf of Mexico sediment trap times series all 11, including non-8 spinose, species show lunar periodicity in at least one size fraction. The scarcity of significant 9 spectral power at the lunar frequency in small-sized foraminifera is in agreement with a high 10 mortality amongst these specimens (Bijma and Hemleben, 1994). Occasional absence in 11 larger specimens also probably reflects failure to detect the lunar signal due to low and 12 intermittent fluxes. In fact, occasional pairing of flux peaks may hint that synchronised flux 13 variability and lunar periodicity could be present, in these size fractions, but poorly and only 14 sporadically expressed. Regardless, our observations of a periodic lunar component in (part 15 of) the flux all species suggests that lunar synchronised reproduction is ubiquitous, rather than 16 the exception in planktonic foraminifera. 17

Lunar periodicity in foraminiferal shell fluxes was up to now only demonstrated for H. 18 pelagica from a single site in the southeast Atlantic Ocean (Lončarić et al., 2005). Despite the 19 high resolution of this study, Lončarić et al. (2005) did not observe lunar periodicity in the 20 shell flux of other species and suggested that lunar synchronised reproduction was unique to 21 H. pelagica. Our data suggest otherwise and we offer two potential reasons why lunar 22 periodicity was not observed in the southeast Atlantic: i) temporal variability expression 23 (spectral power) and ii) obscuration by non-periodic flux variability in certain size fractions. 24 Indeed, significant lunar cyclicity in the Gulf of Mexico time series could in several species 25 only be detected when the size-fractionated data were analysed. Further potential 26 complications in detecting lunar periodicity in the shell flux of planktonic foraminifera could 27 relate to the inherent nature of sediment traps that cannot easily account for differential 28 settling velocity and consequent smearing of the shell fluxes (Takahashi and Bé, 1984) nor for 29 lateral advection of shells over long distances (Von Gyldenfeldt et al., 2000). 30

31

To assess the phasing of the peaks in the shell flux and of reproduction with respect to the 1 lunar cycle, the settling time and life cycle of planktonic foraminifera needs to be taken into 2 account. Sinking speeds of foraminiferal shells vary by an order of magnitude, but are 3 generally between 200 and 500 m day⁻¹ (Takahashi and Bé, 1984). This means that shells 4 most likely arrive within three days after death at the sediment trap at 700 m depth. For 5 specimens that died after gametogenesis this delay is probably even smaller, since several 6 species descend (up to) hundreds of meters in the water column before reproduction (Erez et 7 al., 1991; Hemleben et al., 1989). Because this estimate of settling delay is within the average 8 collecting interval of the sediment traps we do not apply a correction for settling. 9 Furthermore, the time between gametogenesis and death (start of sinking) is most likely very 10 short and insignificant with respect to the average duration of the collecting intervals. Thus, 11 shells that completed their life cycle arrive at the sediment trap shortly after reproduction. 12 The phasing of the flux is similar for most species, with peaks in the shell flux predominantly 13 occurring around or in the week following full moon. Only G. siphonifera and G. calida flux 14 peaks predominantly occur around new moon (table 2, Fig. S3). For some size fractions the 15 number of peaks is low, potentially affecting the estimates of phasing with respect to the lunar 16 cycle, but the general agreement among the timing of the different size fractions indicates that 17 our estimates are robust. Previously, lunar (and semi-lunar) reproductive cycles in G. 18 siphonifera, G. ruber and G. sacculifer were inferred from abundance and size variations 19 (Bijma et al., 1990; Erez et al., 1991). Maxima in the abundance of these species were found 20 to occur 9 to 3 days before full moon, followed by reproduction around full moon (Bijma et 21 al., 1990; Erez et al., 1991). This clearly shows the temporal decoupling between abundance, 22 reproduction and death (i.e. export flux). In the Gulf of Mexico G. ruber (pink and white) and 23 G. sacculifer show a phasing broadly in agreement with the observations in the Red Sea, 24 although a non-negligible part of the flux peaks appears to occur in the week following full 25 moon (table 2). Bijma et al. (1990) also mention in passing that spherical O. universa are 26 most abundant in surface waters off Bermuda and Curaçao around full moon, suggesting a 27 lunar cycle for this species that is in phase with full moon. The maximum in peak occurrence 28 around the same time in the Gulf of Mexico would be consistent with these observations. For 29 The phasing of peaks in G. siphonifera and G. calida is unique among the species analysed 30 here and in the case of G. siphonifera clearly different from that reported by Bijma et al. 31 (1990). Although the delay due to settling may vary among species, such differences are 32

unlikely to explain the difference in phasing of *G. siphonifera*. 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.

7

Whilst the advantage of synchronised reproduction for planktonic foraminfera is obvious, the 8 actual mechanism ensuring lunar synchrony is unclear. In many marine organisms lunar 9 reproduction is thought to be endogenous and possibly phase-locked by an external Zeitgeber 10 (see reviews by Naylor, 2010 and references therein; Neumann, 2014). However, because the 11 reproductive rhythm of *H. pelagica* could be modulated (unpublished results from Hemleben 12 and Spindler, mentioned in Bijma et al. (1990)) and (semi)lunar periodicity in other species 13 was never observed in laboratory conditions, Bijma et al. (1998) argued that in planktonic 14 foraminifera lunar reproduction is caused by an unknown exogenous trigger. Spatial 15 variability in the presence of lunar synchronised reproduction, as suggested by the absence of 16 a lunar rhythm in the shell flux in the southeast Atlantic (Lončarić et al., 2005) in species that 17 show such a rhythm in the Gulf of Mexico, would be in line with such an exogenous 18 mechanism. However, as discussed above, there might be several reasons why lunar 19 periodicity was not detected in the southeast Atlantic time series. 20

Culture studies have shown that reproduction in planktonic foraminifera can be modulated by 21 light and food availability (Bé et al., 1981; Caron et al., 1982), making (changes in) these 22 parameters potential triggers, or environmental cues, for reproduction. If foraminifera had an 23 internal counting mechanism, diurnal light-dark cycles could be a cue for reproduction, albeit 24 an ambiguous one that is sensitive to cloudiness and depth habitat. If food availability were 25 the trigger for reproduction, one would expect lunar periodicity in food availability. While we 26 cannot assess whether or not such a cycle is present in zooplankton abundance, there is no 27 indication that phytoplankton abundance shows such a rhythm (based on spectral analysis of 28 chlorophyll-a concentration, not shown). 29

30 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

32 present and not dependent on seasonal variability. The predominance of reproduction

occurring in around full moon also suggests that most species respond to the same trigger.
However, our dataset 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.

6

Regardless of the exact mechanism, our observations provide strong evidence that 7 synchronised reproduction is common in planktonic foraminifera. Besides having clear 8 benefits for their reproductive success, the lunar periodicity in the shell flux may also affect 9 short-term variability in the total particulate flux from the surface ocean. Planktonic 10 foraminifera are major contributors to the global carbonate flux to the deep ocean (Schiebel, 11 2002) and lunar cyclicity could therefore influence variability of this flux. Little is known 12 about the ballasting potential of foraminifera, but most studies indicate that it is fairly low due 13 to their fast sinking speeds (e.g. Fischer and Karakas, 2009; Schmidt et al., 2014). A direct 14 effect of lunar periodicity on short-term variability of the biological pump is therefore 15 unlikely. However, lunar synchronised reproduction of foraminifera potentially influences the 16 ratio of (particulate) inorganic/organic carbon in the surface ocean and of the total export flux 17 and could in that way contribute to variability in the strength of the biological pump. 18

19

20 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 notion that reproduction
occurs more frequently in large (adult) specimens.

27 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.

29 Only G. siphonifera and G. calida show an opposite pattern, with most shell flux peaks

30 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,

1 clearly demonstrating the importance of a lunar rhythm in determining export flux variability.

2 However, in all species lunar periodicity is superimposed on longer term/seasonal variability

3 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.

6 While the exact mechanism, be it exogenous or endogenous, for lunar periodicity in the shell

7 flux remains unknown, our analysis reveals for the first time that lunar synchronised

8 reproduction is a feature of many species of planktonic foraminifera.

9

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- 25

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

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

4

- 1 Table 2: phasing of lunar cycles in shell fluxes. Phasing determined from counting the
- 2 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
- 4 statistically significant lunar periodicity could be detected.

	>600 µm	500-600	425-500	300-425	212-300	150-212
		μm	μm	μm	μm	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			3, 4	3, 4		
(pink)						
G. ruber					2-4	4
(white)						
<i>P</i> .			3,4	3, 4		
obliquiloculata						
N. dutertrei				3	4	
G. calida			1, 2			
G. glutinata						4

5

1 Fig. 1

2 Planktonic foraminifera shell flux time series separated by size fraction from the northern

3 Gulf of Mexico. Grey curve in the background represents the lunar cycle; NM: new moon;

4 FM: full moon. Lunar periodicity, superimposed on a seasonal cycle, is readily visible in the

- 5 flux of *G. menardii* and *G. siphonifera*.
- 6

7 Fig. 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.

13

14 Fig. 3

15 Temporal expression of lunar periodicity in shell flux of *G. siphonifera* (for other species see

16 Fig. S2). Raw shell flux (grey) overlain with the squared spectral power at the lunar frequency

17 (estimated using continuous Morlet wave transformation, see Material and methods; black).

18 The red dashed line represents the 90 % confidence interval. Lunar periodicity tends to be

19 more expressed (have higher power) when fluxes are higher.

20

21 Fig. 4

Phasing of the lunar cycle in shell fluxes of *G. siphonifera* (for other species see Fig. S3).

23 Histograms of the number of peaks above 10 % of the maximum flux per lunar phase for size

24 fractions where lunar periodicity is statistically significant.

G. menardii



P. obliquiloculata







