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Lunar periodicity in the shell flux of some 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 6 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* and in *Globigerinoides ruber* (both pink and white varieties) is characterised by lunar periodicity. The fluxes of *Pulleniatina obliquiloculata*, *Neogloboquadrina dutertrei*, *Globigerinella calida*, *Globorotalia crassaformis* and *Globigerinita glutinata* do not show significant spectral power at the lunar frequency. If present, 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. Phasing of peak fluxes appears species-specific, with *G. menardii*, *O. universa* and *G. sacculifer* showing most peaks around the full moon and *G. ruber* one week later. Contrastingly, peaks *G. siphonifera* occur dominantly around new moon. Very limited literature exists on lunar phasing of foraminiferal export fluxes, but spatial differences in its presence may exist, corroborating the exogenous nature of lunar synchrony in planktonic foraminifera.

1 Introduction

Planktonic foraminifera reproduce by producing large amounts of gametes (Bé et al., 1977; Spindler et al., 1978). However, concentrations of planktonic foraminifera in the open ocean are generally low (~ 10^1 tests m^{-3}) (Berger, 1969; Field, 2004) reducing the

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chance of reproductive success. Synchronised reproduction would increase the chance of successful gamete fusion 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 five 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 based on repeated plankton tows at a single location Bijma et al. (1990) inferred a lunar reproductive cycle in *G. sacculifer* (confirmed by Erez et al., 1991) and semi-lunar cycles in *G. ruber* and *G. siphonifera*. Lunar periodicity 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) hints at the intermittent presence of a lunar cycle in the fluxes of *G. sacculifer*, *G. ruber*, *O. 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 SE Atlantic Ocean.

Whilst important for the understanding of reproductive strategies of planktonic foraminifera, it remains unresolved if lunar periodicity stems from endogenous or ex-

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ogenous 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 revisit an almost six 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. We find lunar periodicity in the shell flux of *Globorotalia menardii*, *G. siphonifera* (*G. aequilateralis*), *O. universa*, *G. sacculifer* and in *G. ruber* (both pink and white varieties).

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 over 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).

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3 Material and methods

We analyse previously published (2008–2012; Poore et al., 2013; Reynolds et al., 2013) and unpublished (2012–2014) shell flux data (> 150 µm) from a sediment trap time series from the northern Gulf of Mexico (27.5° N, 90.3° W, 700 m water depth) spanning 6 years, mostly at weekly resolution. Full methods are described in Poore et al. (2013). Two gaps in the time series result in an average Nyquist frequency of $\sim 0.05\,\mathrm{day}^{-1}$, which is more than sufficient to resolve lunar cyclicity (period 29.5 days, frequency $0.03\,\mathrm{day}^{-1}$), but insufficient to resolve semi-lunar cycles.

Shell flux time series were analysed by the mid date of the collection interval. Prior to analysis the data were linearly detrended and normalised to unit variance. Spectral analysis was performed in R using REDFIT (Bunn, 2008; R core team, 2013; Schulz and Mudelsee, 2002), which takes reddening of spectrum due to memory effects into account. Continuous Morlet wavelet transform was done on linearly interpolated data (7 day resolution) using the dplR package (Bunn, 2008).

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, which do not allow meaningful spectral analysis.

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 *G. 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 several species. The patterns are most pronounced in *G. menardii* and *G. siphonifera,* which show significant spectral power at the lunar frequency with 99 % confidence; *O. uni-*

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versa, *G. sacculifer* and *G. ruber* (white and pink) also show lunar periodicity, but with a 95 % confidence level (Fig. 2). *G. sacculifer* and *G. ruber* (pink and white) have spectral peaks with power comparable to the lunar cycle close to the lunar frequency band (Fig. 2). The fluxes of *P. obliquiloculata*, *N. dutertrei*, *G. calida*, *G. crassaformis* and *G. glutinata* do not show significant spectral power at the lunar frequency, suggesting little or no influence of the lunar cycle on these species (Fig. 2).

To evaluate the relative influence of flux variability at lunar vs. annual (seasonal) frequency we use the ratio of the square root of the power at lunar over annual frequencies (Table 1). This shows that in these five species the fraction of variance in the shell flux explained by lunar periodicity is > 60 % of that of the annual cycle. In *G. siphonifera* the ratio is > 1, indicating that the lunar cycle has a larger amplitude than the annual/seasonal cycle. This clearly highlights the importance of lunar periodicity on shell flux variability.

Yet it is evident from 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), which seems approximately proportional to the magnitude of the flux.

Peaks in shell fluxes in *G. menardii* dominantly occur around full moon and similar phasing can be seen in in *O. universa* and *G. sacculifer*, which both also show a clear minimum in occurrence of peaks in the week (7.4 days) preceding full moon (Fig. 4). *G. siphonifera* on the other hand shows most peaks in the week around new moon (Fig. 4). The pattern is somewhat less clear in *G. ruber*, but in both the pink and white varieties most peaks occur between full and new moon.

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5 Discussion

Lunar cyclicity in the shell fluxes 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 suggest that a non-calcifying population may survive for several months under unfavourable conditions (Jonkers et al., 2010). The direct effect of a lunar cycle in the shell flux on the sedimentary record however, depends on the relative importance of the lunar vs. the seasonal cycle. In our time series the amount of variance explained by the lunar cycle is on average at least 54 % of, and in the case of *G. menardii* as large as, the seasonal cycle (Table 1). Importantly however, the magnitude/amplitude of the lunar cycle in the shell fluxes varies temporally (Figs. 1 and 3). To a first order the expression of lunar periodicity is related to the magnitude of the shell flux (Fig. 3), illustrating that almost the entire population is affected by the lunar cycle, but also highlighting the importance of the long-term/seasonal cycles in determining variability in the export flux of planktonic foraminiferal shells. However, 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 ratios (Fig. 3). Nevertheless, such temporal variability has not been observed previously and clearly demonstrates the need for long (multi-year) high-resolution shell flux time series to further understand the influence of lunar periodicity on the export of planktonic foraminiferal shell across a range of oceanographic settings.

Our data 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). We also demonstrate lunar periodicity in *G. menardii*, the first time this has been shown for a non-spinose species. Bijma et al. (1990) also 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

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cannot rule out nor confirm these observations. The absence of spectral power at, or close to, the lunar frequency is not easily explained, but is in accordance with previous work. However, occasional pairing of flux peaks may hint that synchronised flux variability and lunar periodicity could in fact be present, but poorly and only intermittently expressed, in these species. Again, high-resolution time series from other locations are required to resolve if lunar cyclicity is really absent from these species. Given the obvious advantages of synchronised reproduction, absence of evidence for short-term periodicity in these species would raise questions about their reproductive strategy.

A further complication in detecting lunar periodicity in the shell flux of planktonic foraminifera relates to the inherent nature of sediment traps that cannot easily account for differential settling velocity and consequent smearing of the shell fluxes (Takahashi and Be, 1984) nor for lateral advection of shells over long distances (Von Gyldenfeldt et al., 2000). The apparent absence of lunar periodicity in the shell fluxes of species, other then *H. pelagica* in the deep SE Atlantic Ocean (Lončarić et al., 2005) is therefore perhaps not unsurprising. However, if correct, it could reflect either the absence of endogenously forced reproductive synchrony or the absence, or only a very weak, exogenous trigger. The results from our study could provide an alternative explanation since we show that lunar periodicity on the shell flux at a site also exhibits substantial temporal variability in amplitude. Such variability may therefore reconcile the contrasting observations from the Red Sea and the SE Atlantic Ocean (Bijma et al., 1990; Erez et al., 1991; Lončarić et al., 2005). Regardless, there is currently no data available to support the hypothesis that there is long-term variability in imprint of the lunar cycle in the planktonic foraminifera population in the SE Atlantic Ocean. The absence of a lunar cycle in the fluxes of *G. ruber*, *G. sacculifer*, *O. universa* and *G. siphonifera* in the latter region therefore implies that the presence of lunar cyclicity is spatially variable, suggesting exogenous forcing (as long as these are really the same species and not different genotypes with different responses) as also suggested from repeated plankton tows and SCUBA collection in the upper water column (Bijma et al., 1990, 1994; Erez et al., 1991; Hemleben et al., 1989).

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There is a clear difference in the phasing of peak fluxes between the different species studied. This is clearest when comparing *G. menardii* and *G. siphonifera*, which show a strong anti-phasing with respect to the lunar cycle (Fig. 4). While settling speeds of foraminiferal shells vary by an order of magnitude, they are generally between 200 and 500 m day^{-1} (Takahashi and Be, 1984) and differences settling time between the two species are unlikely to explain the observed anti-phasing. The observed differences therefore most likely reflect distinctions in response to a lunar phased trigger. Such temporal separation of the flux and hence reproduction is likely to add to the reproductive success as it increases the chances of fusion of gametes of the same species. In the case of *G. ruber* (pink and white) the difference between the number of shell flux peaks occurring around full moon and one week later is very small, but they are consistent between the two varieties, suggesting that the dominant peak timing occurs somewhere between full and new moon (Fig. 4). The generally high sinking speeds of the tests, combined with the fact that some species descend (up to) hundreds of meters in the water column before reproduction (Erez et al., 1991; Hemleben et al., 1989) means that the tests most likely arrive within three days after reproduction at our sediment traps. We therefore apply no correction for settling time and directly compare the observed phasing of peak fluxes with respect to the lunar cycle to other studies. Lunar (and semi-lunar) reproductive cycles in *G. siphonifera*, *G. ruber* and *G. sacculifer* were inferred mainly 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), which may also occur later. However, we observe clearly different phasing for these three species and only the maximum in peak numbers around full moon in *G. sacculifer* is in agreement with previous work. For *G. ruber* and *G. siphonifera* a semi-lunar reproductive cycle was inferred (Bijma et al., 1990). Since lunar periodicity in these species is probably exogenous it could be possible that the phasing differences are due to different expression/power of the trigger of the two

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reproductive events in the lunar cycle in the Red Sea and the Gulf of Mexico. Alternatively, Bijma et al. (1994) argued that the phasing of flux peaks in *G. sacculifer* is a function of reproduction level, where changes in the reproduction level could shift the peak flux from new to full moon and that semi-lunar periodicity could appear at intermediate reproduction levels. Higher resolution time series are needed to disentangle lunar and semi-lunar cycles in these species and to separate differences in forcing from difference in reproduction levels. 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 in line with these observations.

The presence of lunar cyclicity in the export flux of planktonic foraminifera presents strong evidence for synchronised reproduction, which offers these organisms increased chances of reproductive success. However, besides having implications for the reproductive strategy of planktonic foraminifera, 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.

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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* and *G. ruber* (pink and white). No such cycle could be detected in *P. obliquiloculata*, *N. dutertrei*, *G. calida*, *G. crassaformis* or *G. glutinata*. Peaks in the shell flux of *G. menardii, O. universa* and *G. sacculifer* occur predominantly around full moon, whereas those in both varieties of *G. ruber* are more spread out and occur also in the week following full. *G. siphonifera* shows an opposite pattern, with most shell flux peaks occurring around new moon.

Lunar periodicity in these species is superimposed on longer term/seasonal variability in the shell flux and hence is not continuously expressed in the sediment trap time series. The seasonal cycle thus dominates changes in the magnitude of the export flux. However, the amount of variance explained by the lunar cycle is > 50 % of the seasonal cycle and by inference a significant component of its amplitude, clearly illustrating the importance of the lunar cycle in determining variability in the export flux of foraminiferal shells at this site.

Comparison with other sites suggests there may be spatial variability in the presence of lunar cycles in the export flux of *G. ruber*, *G. sacculifer*, *G. siphonifera* and *O. universa*, which, if real, is in line with an exogenous nature of this phenomenon.

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Table 1. Ratio of square root of the power at the lunar and annual frequencies as a measure to compare the variance of the two cycles.

	Lunar/annual power
G. menardii	0.95
G. siphonifera	1.60*
O. universa	0.54
G. sacculifer	0.86
G. ruber (pink)	0.57
G. ruber (white)	0.80

* No clear annual cycle.

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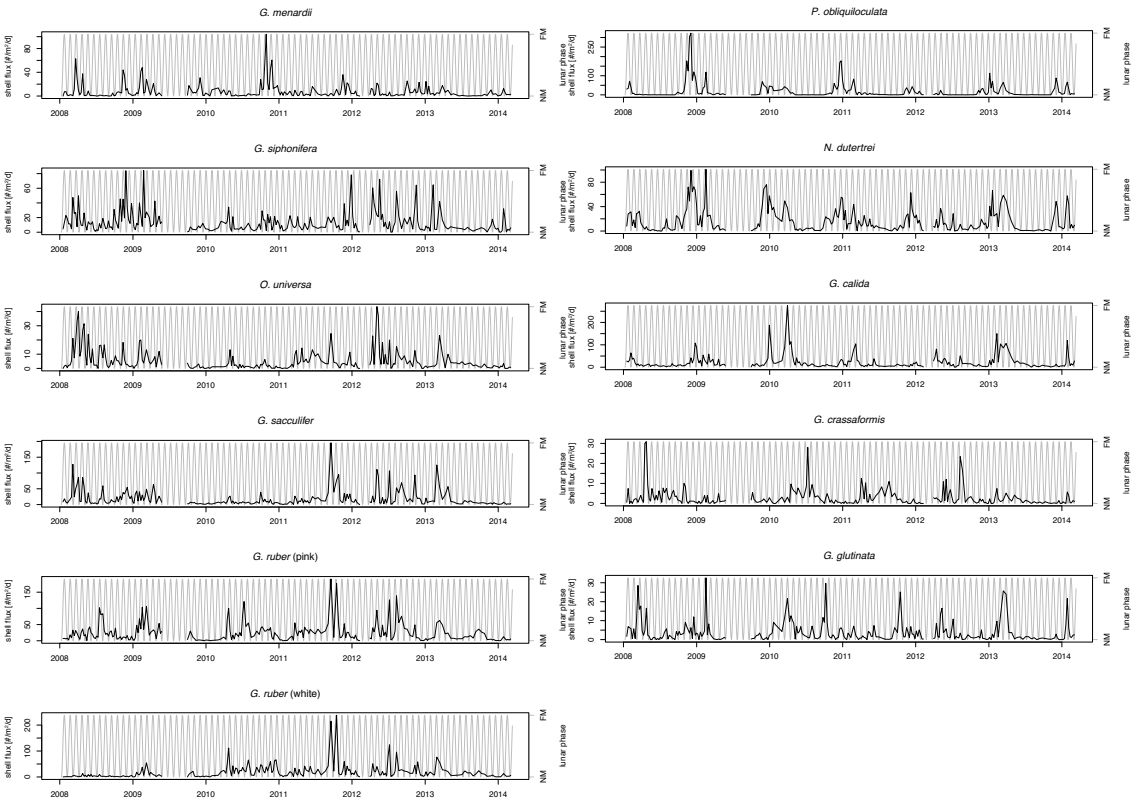

Figure 1. Planktonic foraminifera shell flux time series from the northern Gulf of Mexico. Grey curve in the background represents the lunar cycle; NM: new moon; FM: full moon. Lunar periodicity, superimposed on a seasonal cycle, is readily visible in the flux of *G. menardii* and *G. siphonifera*.

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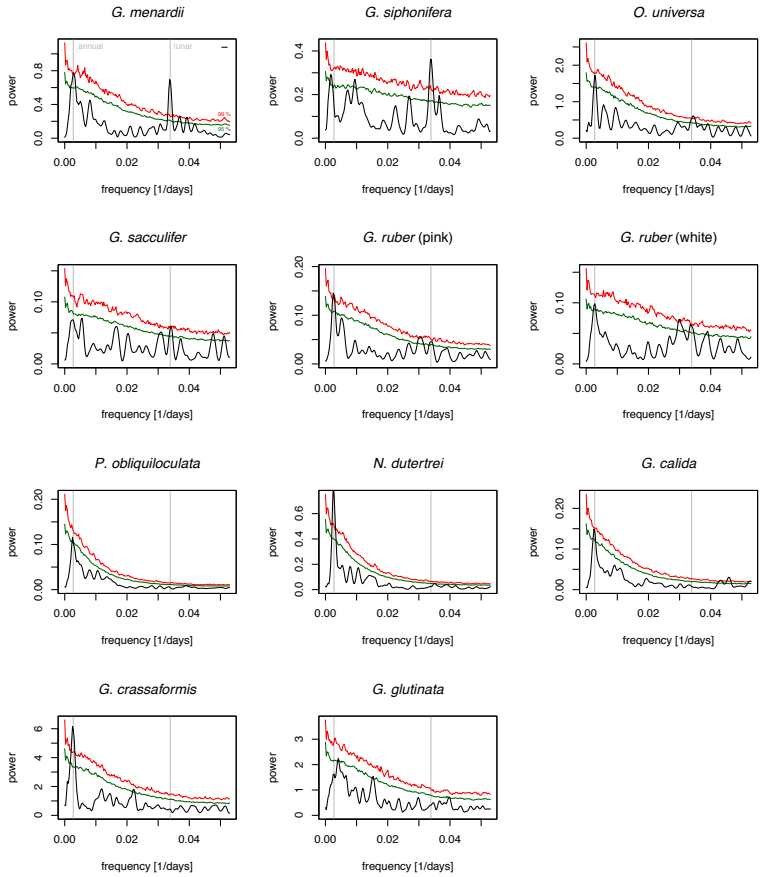

Figure 2. Periodograms of shell flux data shown in Fig. 1. Vertical grey bars denote annual and lunar frequencies. The horizontal black line indicates the 6 dB bandwidth. Red and green lines show 99 and 95 % confidence limits. *G. menardii*, *G. siphonifera*, *O. universa*, *G. sacculifer* and *G. ruber* (pink and white) all show statistically significant power at the lunar frequency.

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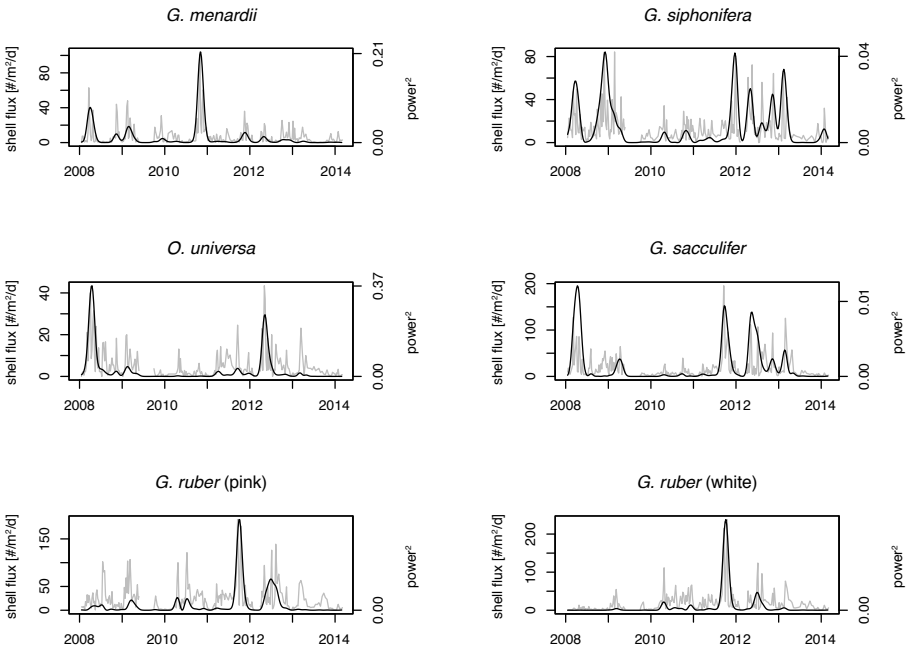

Figure 3. Temporal expression of lunar periodicity in shell fluxes. Raw shell flux (grey) overlain with the squared power of continuous Morlet wave transform at the lunar frequency (black). Lunar periodicity tends to be more expressed (have higher power) when fluxes are higher.

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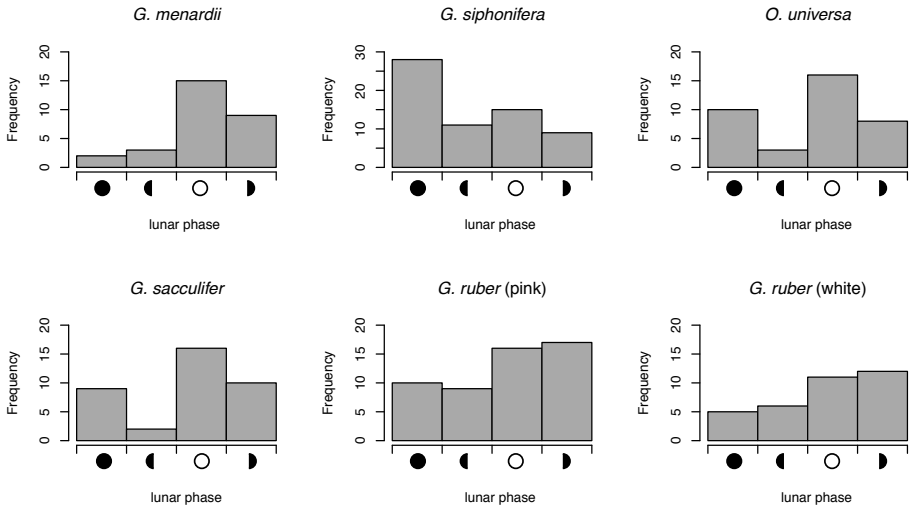

Figure 4. Phasing of the lunar cycle in shell fluxes. Histograms of the number of peaks above 10 % of the maximum flux per lunar phase. *G. menardii*, *O. universa* and *G. sacculifer* dominantly peak around full moon (open circle), whereas *G. siphonifera* shows most peaks around new moon (solid circle). Both varieties of *G. ruber* show most peaks in the week following full moon.

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