

We would like to thank Jelle Bijma for his constructive and timely review of our paper. Below we have copied his comments and provide a response (in red) and propose changes to the manuscript. Following the useful advice from the second reviewer we have analysed the shell fluxes in separate size classes. This revealed that lunar periodicity is in fact present in at least one size fraction in almost all species analysed here. These new findings lead to considerable changes in the revised manuscript. We will append a revised version with all changes highlighted to our response to the second reviewer.

### Review by Jelle Bijma

This paper uses high resolution sediment trap flux data to demonstrate the lunar based reproduction cycle of many species of planktonic Foraminifera. It addresses relevant scientific questions within the scope of BG. Although, the paper does not present novel concepts, ideas or data, it confirms earlier papers and convincingly demonstrates a lunar based reproduction cycle in many species of planktonic Foraminifera. The scientific methods and assumptions are valid and most of it is clearly outlined. The authors give proper credit to related work and clearly indicate their own contribution. The title clearly reflects the contents of the paper and the abstract provides a concise and complete summary. The overall presentation is well structured and clear, and the language fluent and precise. There are a few concepts in the method section that require clarification.

Overall, I rate the scientific significance and quality, as well as the presentation as excellent. Below are some general and more specific comments. Please forgive me when this is "Bijma et al. biased", but we have been looking into planktonic foraminiferal population dynamics at depth (one of the papers you missed: Bijma and Hemleben, 1994).

#### general comments

Except for the first four comments, which I think should be addressed, the rest is cosmetics. Up to the authors. Great paper!

1. The fluxes considered in this study are based on the TOTAL numbers in the size fraction >150  $\mu\text{m}$ . However, total numbers may not be the most sensitive parameter to demonstrate the TIMING of reproduction within the lunar cycle. This can be demonstrated using data on *G. sacculifer*. Bijma et al. (1990; fig. 1) show that the lowest and highest TOTAL abundance are reached between 3-7 days after full moon and about 8 days before full moon, respectively. However, juvenile mortality is very high and an exponential decrease in abundance towards later ontogenetic stages ("larger size fractions") can be observed (see fig. 2 in Bijma and Hemleben, 1994). In fact, the most abundant size fraction in the standing stock in Bijma et al, 1994 is between 100-200  $\mu\text{m}$  (table 2). As a result, the abundance in this size fraction determines the total abundance of *G. sacculifer*. However, in this species gametogenesis is very rare below 250 $\mu\text{m}$  and the percentage of mature specimens, i.e. those that can undergo gametogenesis, increases exponentially between 300 to 400  $\mu\text{m}$  (Bijma and Hemleben, 1994). Hence, the peak of maximum abundance does not coincide with the reproduction event but rather with the result of a reproduction event that must have occurred earlier. Therefore, the reproduction event itself is shifted in time by as much as it takes for the population to grow from zygote to ca. 150 $\mu\text{m}$  plus the time required for this size fraction to settle to 700m water depth (where the sediment trap is placed). For the most abundant fraction (100-200  $\mu\text{m}$ ), the settling velocity is less than 170m/day (Bijma et al., 1994), resulting in a delay of more than 4 days to a trap at 700m. We don't know how long it takes for a zygote to grow to 150 $\mu\text{m}$  but a week seems a reasonable educated guess. Hence, the timing of the reproduction event would be about 11 days before the flux arrives in the trap. I suggest that the authors include something along these lines.

The reviewer makes a valid point with regard to the phasing between abundance and reproduction. However, sediment traps do not register abundance in the water column, but the export flux of dead specimens. Since gametogenesis concludes the life of planktonic foraminifera, the timing of the export flux thus closely tracks reproduction, at least for the specimens that have gone through a complete life cycle.

We have now stressed this point on page 8, line 10-12.

2. A lunar based flux could not be demonstrated for all forams under consideration. However, it seems realistic to assume that ALL planktonic foraminifera must have mechanisms to synchronize their reproduction in time and space! Asexual reproduction has never been observed in planktonic foraminifera. Based on the fact that, in almost 40 years of culture studies, only gametogenesis has

been observed, the assumption that they can only reproduce sexually seems very reasonable. At average densities of ca. 10 specimens/m<sup>3</sup>, and realizing that the gametes of these protists have a limited life-time of ca. 24 hours, during which they do not get dispersed that far from the parent cell, there simply is no other way to explain the dominance of planktonic Foraminifera in pelagic sediments than by a strategy of simultaneous gamete release at a defined point in space and time.

We agree, which is also the reason why we refrained from stating that lunar reproduction was absent in these species in the original submission. However, we have now analysed size fractionated flux data and find lunar periodicity in the one or more size classes in 11 species present in the Gulf of Mexico. These new analyses thus confirm the hypothesis that lunar synchronised reproduction characterises (many species of) planktonic foraminifera.

3. In the method section, please explain the concept of "Nyquist frequency". Further, it was unclear to me how the authors "linearly detrended and normalised to unit variance"? Could you please rephrase? With regard to REDFIT, the authors state "which takes reddening of spectrum due to memory effects into account". It would be good to spend a few words on what that means.

The Nyquist frequency is half the sampling rate; we have replaced this with the average resolution of the time series. To further improve clarity we have added a reference that explains the wavelet transform and changed the section. It now reads (changes in italics):

*'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, 2013; Schulz and Mudelsee, 2002), which uses a first-order autoregressive (AR1) process to account for memory effects associated with autocorrelation in the a 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).'*

4. In the figure caption of Fig. 3 the authors state: "Raw shell flux (grey) overlain with the squared power of continuous Morlet wave transform at the lunar frequency (black)." This should be explained in the main text : What is "the squared power of continuous Morlet wave transform at the lunar frequency"?

Please see our response to the comment above for the changes that will be made to the methodology section. The figure caption has been simplified and now reads:

*'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). Lunar periodicity tends to be more expressed (have higher power) when fluxes are higher.'*

5. All ontogenetic stages within a life cycle of planktonic Foraminifera are found at any time and every depth, and understanding what the majority of the population does, in space and time, can best be resolved by looking at the residuals of the relative frequencies of size classes as a function of time and depth (see Bijma and Hemleben, 1994). If it can be done easily, I suggest to add an additional plot based on Fig. 1 by overlaying the residuals of the fluxes on a lunar basis, i.e. one lunar cycle on the x-axis (1-29.5 days) and average the residuals of six years of lunar months on the y-axis (i.e. the average of each day within a lunar month, normalized to the total flux of that month). I'm not sure if this will improve a conclusion with regard to the timing of maximum flux but it may be worth a try and might even help to resolve semi-lunar cycles (G. ruber; G. siphonifera type 1 and 2?).

The method used by Bijma & Hemleben (1994) applies to plankton net observations and cannot be applied directly to sediment trap data as these do not provide information on the depth distribution of the foraminifera. Nevertheless, we have looked at the residual fluxes, but this does not improve upon the simple method of peak counting which we have applied. We therefore prefer to use the original figure.

Resolving semi-lunar cycles is unfortunately not possible given the resolution of the time series.

6. If possible, it would be interesting to separate the fluxes of *G. trilobus* and *G. sacculifer* sensu stricto. Bijma and Hemleben (1994) found that reproduction of the “sac-like” morphotype was linked to new moon whereas “trilobus” seemed to peak around full moon.

This would indeed be interesting, but unfortunately, we have not separated *G. trilobus* and *G. quadrilobatus* from *G. sacculifer* for the purposes of our census counts.

7. When the authors talk about *G. siphonifera*, can you specify if this is type I or II (see Huber et al., 1997 and Bijma et al., 1998).

As Bijma et al. (1998) and Huber et al. (1997) point out, it is difficult to differentiate between Type I and Type II morphotypes of *G. siphonifera* using empty tests found in sediment traps (as opposed to living specimens used in these studies). The morphometric differences are subtle, and attempting to classify them is likely to prove quite subjective, so we chosen not to attempt differentiation.

8. The authors state that “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.” Maybe it is worth mentioning that therefore this species may be best suited to provide the best annual mean geochemical data for paleo reconstructions (as opposed to species that experience stronger seasonal variability).

It is true that this is the case for *G. siphonifera* in the gulf of Mexico, but Fig. 1 also shows that the its shell flux is far from even throughout the year. Moreover, there is no such thing as a ‘fixed seasonality’, in fact flux-weighted temperature offsets in this species vary between  $-2.5$  and  $4^{\circ}\text{C}$  (Jonkers and Kučera, 2015). It would therefore be misleading to suggest that *G. siphonifera* (or any other species) ‘is best suited to provide the best annual mean geochemical data for paleo reconstructions’. In addition, the geochemistry of this species is significantly affected by differences between type I and II, which are nearly impossible to distinguish in the sediment (Bijma et al., 1998; Huber et al., 1997) and very little geochemical calibration work has been published on *G. siphonifera* up to this point, also arguing against *G. siphonifera* providing the ‘best annual mean geochemical data’. We therefore refrain from including such a statement.

9. Several times in the discussion, the authors refer to the fact “that lunar periodicity on the shell flux at a site also exhibits substantial temporal variability in amplitude.”. I assume that this might be due to temporal differences in mortality during ontogeny (i.e. between the different size classes) which affects the contribution of each size class to the total number of shells collected every week in the trap cups (cf. my first comment).

This simply reflects the fact that the total flux also exhibits variation at other frequencies, such as annual or semi-annual cycles and indeed reflects temporal differences in reproductive success.

#### Technical corrections

1) Page 7; line 14: “and Be, 1984) and differences settling time between the two species are unlikely....” should be “and Be, 1984) and differences in settling time between the two species are unlikely”.

Addressed.

2) In the caption of Fig. 2 it is stated that “The horizontal black line indicates the 6 dB bandwidth”. I do not see this black line?

We have added to the figure caption that the bar is in the upper left panel.

#### References

- Bijma J, Erez J, Hemleben C (1990) Lunar and semi-lunar reproductive cycles in some spinose planktonic foraminifers. *Journal of Foraminiferal Research* 20:117-127
- Bijma J, Hemleben C (1994) Population dynamics of the planktic foraminifer *Globigerinoides sacculifer* (Brady) from the central red sea. *Deep-sea research part I: oceanographic research papers* 41:485-510
- Bijma J, Hemleben C, Wellnitz K (1994) Lunar-influenced carbonate flux of the planktic foraminifer *Globigerinoides sacculifer* (Brady) from the central red sea. *Deep-sea research part I: oceanographic research papers* 41:511-530

Bijma, J., and Hemleben, C.: Population dynamics of the planktic foraminifer *Globigerinoides sacculifer* (Brady) from the central Red Sea, Deep Sea Research Part I: Oceanographic Research Papers, 41, 485-510, [http://dx.doi.org/10.1016/0967-0637\(94\)90092-2](http://dx.doi.org/10.1016/0967-0637(94)90092-2), 1994.

Bijma, J., Hemleben, C., Huber, B. T., Erlenkeuser, H., and Kroon, D.: Experimental determination of the ontogenetic stable isotope variability in two morphotypes of *Globigerinella siphonifera* (d'Orbigny), Marine Micropaleontology, 35, 141-160, [http://dx.doi.org/10.1016/S0377-8398\(98\)00017-6](http://dx.doi.org/10.1016/S0377-8398(98)00017-6), 1998.

Bunn, A. G.: A dendrochronology program library in R (dplR), Dendrochronologia, 26, 115-124, <http://dx.doi.org/10.1016/j.dendro.2008.01.002>, 2008.

Huber, B., Bijma, J., and Darling, K.: Cryptic speciation in the living planktonic foraminifer *Globigerinella siphonifera* (d'Orbigny), Paleobiology, 23, 33-62, 10.1666/0094-8373-23.1.33, 1997.

Jonkers, L., and Kučera, M.: Global analysis of seasonality in the shell flux of extant planktonic foraminifera, Biogeosciences Discuss., 12, 1327-1372, 10.5194/bgd-12-1327-2015, 2015.

Rioul, O., and Vetterli, M.: Wavelets and signal processing, Signal Processing Magazine, IEEE, 8, 14-38, 10.1109/79.91217, 1991.

Schulz, M., and Mudelsee, M.: REDFIT: estimating red-noise spectra directly from unevenly spaced paleoclimatic time series, Computers & Geosciences, 28, 421-426, [http://dx.doi.org/10.1016/S0098-3004\(01\)00044-9](http://dx.doi.org/10.1016/S0098-3004(01)00044-9), 2002.

We would like to thank the reviewer for their thorough review of our paper. The first comment, to investigate size specific data, has proved particularly insightful. These new analyses show that lunar periodicity in the shell flux is in fact present in almost all species, although not in all size fractions. The new results from the analysis of the size data strengthened and extended our initial conclusions, but also required many changes to the manuscript. These have all been highlighted in the version appended below. Below we have copied the comments and provided a response (in red).

This paper describe lunar periodicity of shell flux of modern planktic foraminifers recovered by sediment trap experiments in the Gulf of Mexico. General ecology of planktic foraminifera is reported by many papers, but especially, the reproductive phase/periodicity is still poorly known. This manuscript will provide a new information about lunar and semi-lunar periodicity of some planktic foraminiferal species in the subtropical realm of the Gulf of Mexico. Time resolution of this study is extremely high (weekly resolution!) compared with previous related studies by moored time-series sediment traps, and it should have a potential to resolve enigmatic planktic foraminiferal ecology. On the other hand, I think that the information to discuss about the reproductive periodicity and their ecological relationships are insufficient. A part of the assemblage data as a base of this manuscript is excellent and it has already published some reviewed journal/reports, so the quality of assemblage data is sufficient.

Comment1: The authors defined that empty shell flux of planktic foraminifera is the reproductive individual, however the shell length (size) of each species does not shown. How does the authors define the adult (reproduced) specimen? Individuals larger than 150  $\mu$ m include not only adult specimen but also immature (pre-reproduced) specimen. For instance, *G. siphonifera* and *G. sacculifer* in the tropical-subtropical regions become larger than 700  $\mu$ m. Although the separation of the reproduced specimen is difficult by only the shell length in general, it is the one of the key factors. It should be shown size distributions of each species as the basic dataset.

This is a valid point and the suggestion to investigate the size distribution of the shells has proven to be very valuable indeed. For the Gulf of Mexico time series size-fractionated data are available for the period from 2010 to 2014. Analysis of these data supports our initial findings and even shows lunar cyclicity in more species than previously observed. In the revised version of the manuscript we have therefore limited our analysis/discussion to the period where size data are available.

These new analyses show that lunar periodicity is mostly present in the larger size fractions, suggesting that the cyclicity indeed reflects synchronized reproductive behavior. In this respect it should however be noted that while the proportion of individuals that have undergone gametogenesis increases with size, larger specimens are also less abundant (i.e. their flux is more pulsed). This makes it challenging, if not impossible, to determine the power spectrum of the flux of the largest tests.

In addition, tests of *G. sacculifer* with sac-like chambers were observed in the <300  $\mu$ m fraction, providing evidence that gametogenesis does also occur in the smaller size fractions and thus corroborating that the lunar cycle in the flux does indeed reflect reproduction.

We added this on page 6, line 6-9.

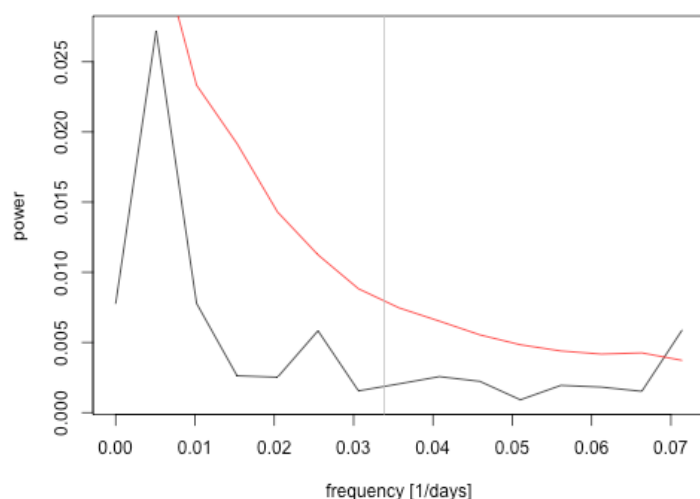
We have made some important changes to the manuscript to accommodate the size specific data. These changes are highlighted in the document attached below.

Comment2: Lateral transportation of biological particles is the most concerning issue of this manuscript. The Gulf of Mexico is very famous place of deep-sea turbidites/landslides. The location of sediment trap used in this study was very close to the large continental shelf (probably less than 100km as direct distance?), therefore sinking particles may be possibly disturbed by deep-sea turbidites and related material transportations. Especially I'm concerning that fluctuation of sea tide synchronize to the lunar periodicity, therefore material transportation also occur at the same timing. In this case, shell flux of some planktic forms may look increasing apparently during full/new moon phases. It is needed to exclude or discuss the possibility of lateral transportation of shells. And if

available, please add current direction/speed data through the whole observation periods. In addition, lithologic material data is also important.

The reviewer rightly points out the possibility of tidally influenced lateral transport. However, for a number of reasons it is unlikely that such lateral transport affected the periodicity of the planktonic foraminifera fluxes:

1. If the fluxes were tidally forced one would expect all species to show the same pattern. However:
  - a. Not all size fractions show lunar periodicity and those that show it have different power in the lunar frequency band (Fig. 2).
  - b. The phasing is different amongst species (Fig. 4)
  - c. The temporal pattern of spectral power in the lunar frequency band is different for each species (Fig 3).
2. We observe lunar cyclicity in the shell flux, yet spring and neap tidal cycles, which could potentially have influenced lateral transport, have a semi-lunar periodicity.
3. Since the trap is moored 400 m above the sea floor the influence of resuspended material is likely to be negligible. While lithogenic flux data are only available for January through July 2008 ( $n = 28$ ), its spectrogram does not show any sign of lunar periodicity (grey line in figure below; the red line is the 95 % confidence interval).



We have added the following paragraph to the start of the discussion to explain why we think the flux time series represents a primary signal that is not affected by tidally-synchronised advection of foraminifera shells:

‘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. 4) and the different temporal evolution of variance in the lunar frequency band (Fig. 3) indicate that this periodicity is not due to tidally synchronised lateral advection of shells, but instead reflects a primary signal in the shell flux 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 the proportion of specimens that have undergone gametogenesis increases with size (Bé et al., 1981; Bijma and Hemleben, 1994). The presence of sac-like chambers in *G. sacculifer*, unambiguous evidence of gametogenesis (Hemleben et al., 1989), in the fine fraction of this species supports the reproductive nature of the lunar periodicity in the shell fluxes.’

Comment3: The authors described that lunar periodicity comes from exogenous nature in planktic foraminifera. What kind of exogenous “factors”? I think the ecological information and description of

planktic forms are absolutely lacking in this manuscript. For example, metabolism of cell inducing gamete creation in living planktic foraminifera is probably related to temperature, food availability, and light intensity (for symbiont bearing species) etc. The authors should show some possibility /hypothesis from the many observable oceanographic environmental factors to make breakthrough of living planktic foraminiferal ecological studies. Lunar /semi-lunar periodicity of reproduction of planktic foraminifera was already described by several authors, so it is lack of novelty.

We fully acknowledge that lunar reproduction is not a new concept, as we have highlighted in the introduction and discussion of the manuscript. However, the novelty of our study is that it demonstrates lunar periodicity in the shell flux for a large number of species. Up to now evidence for such periodicity in the shell flux was only described for *H. pelagica* (Lončarić et al., 2005) and in fact our data demonstrate that many more species than previously thought are characterized by lunar reproduction.

While the sequence of events leading/changes in the test prior to gametogenesis is well described and some studies have addressed factors that may influence reproduction in planktonic foraminifera, the actual trigger for gametogenesis is still unknown. Unfortunately, the available data do not allow us to fully address this issue and therefore any suggestion for a potential mechanism driving lunar reproduction must remain speculative. However, we have added the following paragraphs to offer some suggestions and discussion address this issue. This is clearly a topic for future studies:

‘Whilst the advantage of synchronised reproduction for planktonic foraminifera 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. (1998) argued that in planktonic foraminifera lunar reproduction is caused by an unknown endogenous 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 southeast Atlantic (Lončarić et al., 2005) in species that show such rhythm in the Gulf of Mexico, would be in line with such an exogenous trigger. However, as discussed above, there could be several reasons why lunar periodicity was not detected in the southeast 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 cues, for reproduction. If foraminifera had some 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 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. More studies, both in the field and in the laboratory, are needed to elucidate the cause of (semi)lunar reproductive synchrony in planktonic foraminifera.’

Minor items:

1) Indices of all figures should be used more larger characters.

Done.

2) Information of methodology are not sufficient: For example, information of sample collections, deployed periods, methodology of counts of foram shells etc. (e.g. A McLane PARFLUX Mark 78



automated sediment trap was deployed in early January 2008 in approximately 1,150 meters (m) of water depth at approximately 27.5 oN latitude and 90.3 oW longitude. The trap is equipped with 21 collection cups that are mounted on a rotating plate that is programmed to rotate every 7 or 14 days: : ...)

We will add additional information to the method section, but for an extended description of the methodology we refer to Poore et al. (2013) and Reynolds et al. (2013).

3) Please check the spelling of Prof. Bé.

Done.

4) p17194: other “than”?

Addressed.

Bé, A. W. H., Caron, D. A., and Anderson, O. R.: Effects of feeding frequency on life processes of the planktonic foraminifer *Globigerinoides sacculifer* in laboratory culture, *Journal of the Marine Biological Association of the United Kingdom*, 61, 257-277, doi:10.1017/S002531540004604X, 1981.

Bijma, J., and Hemleben, C.: Population dynamics of the planktic foraminifer *Globigerinoides sacculifer* (Brady) from the central Red Sea, *Deep Sea Research Part I: Oceanographic Research Papers*, 41, 485-510, [http://dx.doi.org/10.1016/0967-0637\(94\)90092-2](http://dx.doi.org/10.1016/0967-0637(94)90092-2), 1994.

Lončarić, N., Brummer, G.-J. A., and Kroon, D.: Lunar cycles and seasonal variations in deposition fluxes of planktic foraminiferal shell carbonate to the deep South Atlantic (central Walvis Ridge), *Deep Sea Research Part I: Oceanographic Research Papers*, 52, 1178-1188, <http://dx.doi.org/10.1016/j.dsr.2005.02.003>, 2005.

Poore, R. Z., Tedesco, K. A., and Spear, J. W.: Seasonal Flux and Assemblage Composition of Planktic Foraminifers from a Sediment-Trap Study in the Northern Gulf of Mexico, *Journal of Coastal Research*, 63, 6-19, 10.2112/si63-002.1, 2013.

Reynolds, C. E., Richey, J. N., and Poore, R. Z.: Seasonal flux and assemblage composition of planktic foraminifera from the northern Gulf of Mexico, 2008-2012, Reston, Virginia, 13, 2013.



# 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

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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 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 et 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 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 *Neoglobobulimina pachyderma* (Volkman, 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*, *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

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**Deleted:** 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 shell flux of any other species present at the sediment trap site in the southeast Atlantic  
2 Ocean.

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

13

## 14 2 Hydrographic setting

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

27

## 28 3 Material and methods

29 We analyse previously published (2010-2012; Reynolds et al., 2013) and unpublished (2012-  
30 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

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**Deleted:** 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)

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1 weekly resolution. Full methods [on the sediment trap mooring and foraminifera analysis](#) are  
2 described in Poore et al. (2013) [and Reynolds et al. \(2013\)](#). [Shell fluxes are separated in six](#)  
3 [sieve size fractions \(150-212  \$\mu\text{m}\$ , 212-300  \$\mu\text{m}\$ , 300-425  \$\mu\text{m}\$ , 425-500  \$\mu\text{m}\$ , 500-600  \$\mu\text{m}\$  and](#)  
4 [>600  \$\mu\text{m}\$ \)](#).  
5 [The average sampling resolution of the time series is ~9 days, which is more than sufficient to](#)  
6 [resolve lunar cyclicity \(period 29.5 days\), but insufficient to resolve semi-lunar cycles. Each](#)  
7 [size-specific time series was analysed by the mid date of the collection interval. Prior to](#)  
8 [analysis linear trends in the data were removed and all fluxes were normalised to unit](#)  
9 [variance. Spectral analysis was performed in R using REDFIT \(Bunn, 2008; R core team,](#)  
10 [2013; Schulz and Mudelsee, 2002\), which uses a first-order autoregressive \(AR1\) process to](#)  
11 [account for memory effects associated with autocorrelation in the a time series to estimate](#)  
12 [spectral peak significance. To estimate the temporal patterns of spectral power in the lunar](#)  
13 [frequency band, continuous Morlet wavelet transform was performed on linearly interpolated](#)  
14 [data \(7 day resolution\) using the dplR package \(Bunn, 2008; Rioul and Vetterli, 1991\).](#)  
15 Data from *Globorotalia truncatulinoides*, *G. bulloides* and *Globigerina falconensis* were not  
16 analysed since these species show only very brief pulses of high shell flux in winter,  
17 precluding meaningful spectral analysis. [Such intermittency of the flux was also the case for](#)  
18 [some size classes, particularly the largest and smallest, in several species. These cases have](#)  
19 [not been analysed and are indicated in table 1.](#)

20

## 21 4 Results

22 All species show (quasi) seasonal variations in the shell flux (Fig. 1). Superimposed on the  
23 seasonal cycle, many species show higher frequency variability and lunar periodicity is  
24 readily apparent in several species (Fig. 1). This is clearest in the shell flux of *Globorotalia*  
25 *menardii*, which peaks around full moon and *G. siphonifera*, which seems to peak  
26 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](#)  
28 [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](#)  
30 [the remaining species in tables 1 and 2 \(associated figures for all species can be found in the](#)  
31 [supplement to this paper\).](#) The patterns are most pronounced in *G. menardii* and *G.*

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*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 time scale, seasonal variance is very small (Fig. 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 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 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

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**Deleted:** *O. universa*, *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*, *calida*, *crassaformis* and *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) ... [2]

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1 this periodicity is not due to tidally synchronised lateral advection of shells, but instead  
 2 reflects a primary signal in the shell flux, most likely related to the reproductive cycle. The  
 3 tendency for lunar periodicity to be more present in larger shells also supports that the  
 4 periodicity reflects reproductive synchronisation, since it has previously been shown that the  
 5 proportion of specimens that have undergone gametogenesis increases with size (Bé et al.,  
 6 1981; Bijma and Hemleben, 1994). Moreover, the presence of sac-bearing *G. sacculifer*,  
 7 which must have undergone gametogenesis (Hemleben et al., 1989), in the fine fraction of  
 8 this species further corroborates the reproductive nature of the lunar periodicity in the shell  
 9 fluxes.

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

25 The potential importance of lunar cyclicity in the fossil record ultimately depends on the  
 26 relative importance of the lunar versus long-term/seasonal cycle. In some species – and in  
 27 some size fractions – the ratio of spectral power in the lunar and seasonal frequency is close  
 28 to, or greater than, one (e.g. *G. siphonifera* and *G. menardii*; Fig. 2 and S1) highlighting the  
 29 importance of lunar cyclicity in shell flux variance in these species. In most other species  
 30 however, there is more spectral power in the seasonal band. Together with the covariability  
 31 between shell flux and lunar cycle amplitude, this demonstrates the importance of the long-

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1 term/seasonal cycles in the shell flux for the fossil signal of planktonic foraminifera (cf.  
2 Jonkers and Kučera, 2015).

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

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

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**Moved up [3]:** Bijma et al. (1990) also 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. The absence of spectral power at, or close to, the lunar frequency is not easily explained, but is in accordance with previous work. However

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**Deleted:** 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.



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<sup>-1</sup> (Takahashi and Bé, 1984). This means that shells most likely arrive within three 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 meters 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. For 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

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**Moved down [2]:** 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; Bijma et al., 1994; Erez et al., 1991; Hemleben et al., 1989).

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**Deleted:** The apparent absence of lunar periodicity in the shell fluxes of species, other than *H. pelagica* in the deep SE Atlantic Ocean 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; Bijma et al., 1994; Erez et al., 1991; Hemleben et al., 1989).

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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.

Whilst the advantage of synchronised reproduction for planktonic foraminifera 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. (1998) 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 southeast 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 southeast 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

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**Moved down [5]:** 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 reproductive events in the lunar cycle in the Red Sea and the Gulf of Mexico.

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**Deleted:** 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.

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.

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 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.

Lukas Jonkers 28/4/2015 18:28

**Moved up [4]:** 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.

Lukas Jonkers 28/4/2015 19:10

**Deleted:** 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.

Lukas Jonkers 28/4/2015 14:34

**Moved (insertion) [2]**

Lukas Jonkers 28/4/2015 19:24

**Deleted:** 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 ... [6]

Lukas Jonkers 28/4/2015 18:29

**Moved (insertion) [5]**

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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.

## Acknowledgements

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## References

- Almogi-Labin, A.: Population dynamics of planktic Foraminifera and Pteropoda—Gulf of Aqaba, Red Sea, Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series B, 87, 481-511, 1984.
- Bé, A. W. H., Hemleben, C., Anderson, O. R., Spindler, M., Hacunda, J., and Tuntivate-Choy, S.: Laboratory and field observations of living planktonic foraminifera, Micropaleontology, 23, 155-179, 1977.
- Bé, A. W. H., Caron, D. A., and Anderson, O. R.: Effects of feeding frequency on life processes of the planktonic foraminifer Globigerinoides sacculifer in laboratory culture, Journal of the Marine Biological Association of the United Kingdom, 61, 257-277, doi:10.1017/S002531540004604X, 1981.
- Bemis, B. E., Spero, H. J., Bijma, J., and Lea, D. W.: Reevaluation of the Oxygen Isotopic Composition of Planktonic Foraminifera: Experimental Results and Revised Paleotemperature Equations, Paleoceanography, 13, 150-160, 10.1029/98pa00070, 1998.

Lukas Jonkers 29/4/2015 12:39

**Deleted:** the amount of variance explained by the lunar 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.

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Lukas Jonkers 29/4/2015 13:27

**Deleted:** 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.

1 Berger, W. H.: Ecologic patterns of living planktonic Foraminifera, Deep Sea Research and  
2 Oceanographic Abstracts, 16, 1-24, [http://dx.doi.org/10.1016/0011-7471\(69\)90047-3](http://dx.doi.org/10.1016/0011-7471(69)90047-3), 1969.

3 Bijma, J., Erez, J., and Hemleben, C.: Lunar and semi-lunar reproductive cycles in some  
4 spinose planktonic foraminifers, Journal of Foraminiferal Research, 20, 117-127, 1990.

5 Bijma, J., and Hemleben, C.: Population dynamics of the planktic foraminifer  
6 *Globigerinoides sacculifer* (Brady) from the central Red Sea, Deep Sea Research Part I:  
7 Oceanographic Research Papers, 41, 485-510, [http://dx.doi.org/10.1016/0967-0637\(94\)90092-2](http://dx.doi.org/10.1016/0967-0637(94)90092-2),  
8 1994.

9 Bijma, J., Hemleben, C., and Wellnitz, K.: Lunar-influenced carbonate flux of the planktic  
10 foraminifer *Globigerinoides sacculifer* (Brady) from the central Red Sea, Deep Sea Research  
11 Part I: Oceanographic Research Papers, 41, 511-530, [http://dx.doi.org/10.1016/0967-](http://dx.doi.org/10.1016/0967-0637(94)90093-0)  
12 [0637\(94\)90093-0](http://dx.doi.org/10.1016/0967-0637(94)90093-0), 1994.

13 Bunn, A. G.: A dendrochronology program library in R (dplR), Dendrochronologia, 26, 115-  
14 124, <http://dx.doi.org/10.1016/j.dendro.2008.01.002>, 2008.

15 Caron, D. A., Bé, A. W. H., and Anderson, O. R.: Effects of variations in light intensity on  
16 life processes of the planktonic foraminifer *Globigerinoides sacculifer* in laboratory culture,  
17 Journal of the Marine Biological Association of the United Kingdom, 62, 435-451,  
18 doi:10.1017/S0025315400057374, 1982.

19 Erez, J., Almogi-Labin, A., and Avraham, S.: On the Life History of Planktonic Foraminifera:  
20 Lunar Reproduction Cycle in *Globigerinoides sacculifer* (Brady), Paleoceanography, 6, 295-  
21 306, 10.1029/90pa02731, 1991.

22 Field, D. B.: Variability in vertical distributions of planktonic foraminifera in the California  
23 Current: Relationships to vertical ocean structure, Paleoceanography, 19, PA2014,  
24 10.1029/2003pa000970, 2004.

25 Fischer, G., and Karakaş, G.: Sinking rates and ballast composition of particles in the Atlantic  
26 Ocean: implications for the organic carbon fluxes to the deep ocean, Biogeosciences, 6, 85-  
27 102, 10.5194/bg-6-85-2009, 2009.

28 Hemleben, C., Spindler, M., and Anderson, O. R.: Modern Planktonic Foraminifera, Springer  
29 Verlag, Berlin, 1989.

30 Jonkers, L., Brummer, G.-J. A., Peeters, F. J. C., van Aken, H. M., and De Jong, M. F.:  
31 Seasonal stratification, shell flux, and oxygen isotope dynamics of left-coiling *N. pachyderma*  
32 and *T. quinqueloba* in the western subpolar North Atlantic, Paleoceanography, 25, PA2204;  
33 doi:2210.1002/palo.20018, 2010.

1 Jonkers, L., and Kučera, M.: Global analysis of seasonality in the shell flux of extant  
2 planktonic Foraminifera, *Biogeosciences*, 12, 2207-2226, 10.5194/bg-12-2207-2015, 2015.

3 Kawahata, H., Nishimura, A., and Gagan, M. K.: Seasonal change in foraminiferal production  
4 in the western equatorial Pacific warm pool: evidence from sediment trap experiments, *Deep*  
5 *Sea Research Part II: Topical Studies in Oceanography*, 49, 2783-2800,  
6 [http://dx.doi.org/10.1016/S0967-0645\(02\)00058-9](http://dx.doi.org/10.1016/S0967-0645(02)00058-9), 2002.

7 Lončarić, N., Brummer, G.-J. A., and Kroon, D.: Lunar cycles and seasonal variations in  
8 deposition fluxes of planktic foraminiferal shell carbonate to the deep South Atlantic (central  
9 Walvis Ridge), *Deep Sea Research Part I: Oceanographic Research Papers*, 52, 1178-1188,  
10 <http://dx.doi.org/10.1016/j.dsr.2005.02.003>, 2005.

11 Naylor, E.: Lunar and semilunar biorhythms, in: *Chronobiology of Marine Organisms*, edited  
12 by: Naylor, E., Cambridge University Press, Cambridge, 89-115, 2010.

13 Neumann, D.: Timing in Tidal, Semilunar, and Lunar Rhythms, in: *Annual, Lunar, and Tidal*  
14 *Clocks*, edited by: Numata, H., and Helm, B., Springer Japan, 3-24, 2014.

15 Poore, R. Z., Tedesco, K. A., and Spear, J. W.: Seasonal Flux and Assemblage Composition  
16 of Planktic Foraminifers from a Sediment-Trap Study in the Northern Gulf of Mexico,  
17 *Journal of Coastal Research*, 63, 6-19, 10.2112/si63-002.1, 2013.

18 R core team: R: A language and environment for statistical computing, 2013.

19 Reynolds, C. E., Richey, J. N., and Poore, R. Z.: Seasonal flux and assemblage composition  
20 of planktic foraminifera from the northern Gulf of Mexico, 2008-2012, Reston, Virginia, 13,  
21 2013.

22 Rioul, O., and Vetterli, M.: Wavelets and signal processing, *Signal Processing Magazine*,  
23 *IEEE*, 8, 14-38, 10.1109/79.91217, 1991.

24 Schiebel, R., Bijma, J., and Hemleben, C.: Population dynamics of the planktic foraminifer  
25 *Globigerina bulloides* from the eastern North Atlantic, *Deep Sea Research Part I:*  
26 *Oceanographic Research Papers*, 44, 1701-1713, 10.1016/s0967-0637(97)00036-8, 1997.

27 Schiebel, R.: Planktic foraminiferal sedimentation and the marine calcite budget, *Global*  
28 *Biogeochemical Cycles*, 16, 1065, 10.1029/2001gb001459, 2002.

29 Schmidt, K., De La Rocha, C. L., Gallinari, M., and Cortese, G.: Not all calcite ballast is  
30 created equal: differing effects of foraminiferan and coccolith calcite on the formation and  
31 sinking of aggregates, *Biogeosciences*, 11, 135-145, 10.5194/bg-11-135-2014, 2014.

1 Schulz, M., and Mudelsee, M.: REDFIT: estimating red-noise spectra directly from unevenly  
2 spaced paleoclimatic time series, *Computers & Geosciences*, 28, 421-426,  
3 [http://dx.doi.org/10.1016/S0098-3004\(01\)00044-9](http://dx.doi.org/10.1016/S0098-3004(01)00044-9), 2002.

4 Spindler, M., Anderson, O. R., Hemleben, C., and Bé, A. W. H.: Light and Electron  
5 Microscopic Observations of Gametogenesis in *Hastigerina pelagica* (Foraminifera)\*, *The*  
6 *Journal of Protozoology*, 25, 427-433, 10.1111/j.1550-7408.1978.tb04164.x, 1978.

7 Spindler, M., Hemleben, C., Bayer, U., Bé, A., and Anderson, O.: Lunar periodicity of  
8 reproduction in the planktonic foraminifer *Hastigerina pelagica*, *Marine Ecology Progress*  
9 *Series*, 1, 61-64, 1979.

10 Takahashi, K., and Bé, A. W. H.: Planktonic foraminifera: factors controlling sinking speeds,  
11 *Deep Sea Research Part A. Oceanographic Research Papers*, 31, 1477-1500, 10.1016/0198-  
12 0149(84)90083-9, 1984.

13 Volkmann, R.: Planktic foraminifers in the outer Laptev Sea and the Fram Strait - modern  
14 distribution and ecology, *The Journal of Foraminiferal Research*, 30, 157-176,  
15 10.2113/0300157, 2000.

16 Von Gyldenfeldt, A.-B., Carstens, J., and Meincke, J.: Estimation of the catchment area of a  
17 sediment trap by means of current meters and foraminiferal tests, *Deep Sea Research Part II:*  
18 *Topical Studies in Oceanography*, 47, 1701-1717, 2000.

19 Vukovich, F. M., and Maul, G. A.: Cyclonic eddies in the eastern Gulf of Mexico, *Journal of*  
20 *Physical Oceanography*, 15, 105-117, 1985.

21 Vukovich, F. M.: Climatology of Ocean Features in the Gulf of Mexico Using Satellite  
22 Remote Sensing Data, *Journal of Physical Oceanography*, 37, 689-707, 10.1175/jpo2989.1,  
23 2007.

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25



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

	>600 $\mu\text{m}$	500-600 $\mu\text{m}$	425-500 $\mu\text{m}$	300-425 $\mu\text{m}$	212-300 $\mu\text{m}$	150-212 $\mu\text{m}$
<i>G. menardii</i>	<u>Y</u>	<u>Y</u>	<u>Y</u>	<u>Y</u>	<u>Y</u>	<u>Y</u>
<i>G. siphonifera</i>	<u>Y</u>	<u>Y</u>	<u>Y</u>	<u>N</u>	<u>N</u>	<u>N</u>
<i>O. universa</i>	<u>N</u>	<u>Y</u>	<u>Y</u>	<u>N</u>	<u>na</u>	<u>na</u>
<i>G. sacculifer</i>	<u>N</u>	<u>N</u>	<u>N</u>	<u>Y</u>	<u>Y</u>	<u>N</u>
<i>G. ruber</i> (pink)	<u>na</u>	<u>N</u>	<u>Y</u>	<u>Y</u>	<u>N</u>	<u>N</u>
<i>G. ruber</i> (white)	<u>na</u>	<u>na</u>	<u>N</u>	<u>N</u>	<u>Y</u>	<u>Y</u>
<i>P. obliquiloculata</i>	<u>na</u>	<u>N</u>	<u>Y</u>	<u>Y</u>	<u>N</u>	<u>N</u>
<i>N. dutertrei</i>	<u>na</u>	<u>na</u>	<u>N</u>	<u>Y</u>	<u>Y</u>	<u>N</u>
<i>G. calida</i>	<u>na</u>	<u>na</u>	<u>Y</u>	<u>N</u>	<u>N</u>	<u>N</u>
<i>G. crassaformis</i>	<u>na</u>	<u>na</u>	<u>N</u>	<u>N</u>	<u>N</u>	<u>N</u>
<i>G. glutinata</i>	<u>na</u>	<u>na</u>	<u>na</u>	<u>na</u>	<u>N</u>	<u>Y</u>

Lukas Jonkers 28/4/2015 10:24

**Deleted:** 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. ... [9]

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:  
3 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.

	<u>&gt;600 <math>\mu\text{m}</math></u>	<u>500-600 <math>\mu\text{m}</math></u>	<u>425-500 <math>\mu\text{m}</math></u>	<u>300-425 <math>\mu\text{m}</math></u>	<u>212-300 <math>\mu\text{m}</math></u>	<u>150-212 <math>\mu\text{m}</math></u>
<u><i>G. menardii</i></u>	<u>3, 4</u>	<u>3</u>	<u>3, 4</u>	<u>4</u>	<u>3</u>	<u>3</u>
<u><i>G. siphonifera</i></u>	<u>1</u>	<u>1</u>	<u>1</u>			
<u><i>O. universa</i></u>		<u>3</u>	<u>4</u>			
<u><i>G. sacculifer</i></u>				<u>3, 4</u>	<u>4</u>	
<u><i>G. ruber</i> (pink)</u>			<u>3, 4</u>	<u>3, 4</u>		
<u><i>G. ruber</i> (white)</u>					<u>2-4</u>	<u>4</u>
<u><i>P.</i> <i>obliquiloculata</i></u>			<u>3, 4</u>	<u>3, 4</u>		
<u><i>N. dutertrei</i></u>				<u>3</u>	<u>4</u>	
<u><i>G. calida</i></u>			<u>1, 2</u>			
<u><i>G. glutinata</i></u>						<u>4</u>

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

8 Periodograms of the size-fractionated shell flux time series of *G. siphonifera* (for other  
9 species see Fig. S1). Vertical grey bars denote annual and lunar frequencies. The horizontal  
10 black line in the upper left panel indicates the 6 dB bandwidth. Red and green lines show 99  
11 % and 95 % confidence limits. Lunar periodicity is clearly present in the three largest size  
12 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

22 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.

Lukas Jonkers 29/4/2015 14:18

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Lukas Jonkers 29/4/2015 14:19

**Deleted:** *G. menardii*, *G. siphonifera*, *O. universa*, *G. sacculifer* and *G. ruber* (pink and white) all show statistically significant power at the lunar frequency.

Lukas Jonkers 29/4/2015 14:19

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**Deleted:** *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.

Shell flux

*O. universa*, *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*, *calida*, *crassaformis* and *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.

Peaks in shell fluxes in *G. menardii* dominantly occur around full moon and similar phasing can be seen 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

but also highlighting the importance of the long-term/seasonal cycles in determining variability in the export flux of planktonic foraminiferal shells. 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).

However, t

The apparent absence of lunar periodicity in the shell fluxes of species, other than *H. pelagica* in the deep SE Atlantic Ocean 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; Bijma et al., 1994; Erez et al., 1991; Hemleben et al., 1989).

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<sup>-1</sup> (Takahashi and Bé, 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.

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Lukas Jonkers

28/04/2015 19:24

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; Bijma et al., 1994; Erez et al., 1991; Hemleben et al., 1989).

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 reproductive events in the lunar cycle in the Red Sea and the Gulf of Mexico.

The presence of lunar cyclicity in the export flux of planktonic foraminifera presents

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, which offers these organisms increased chances of reproductive success. However, besides

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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.

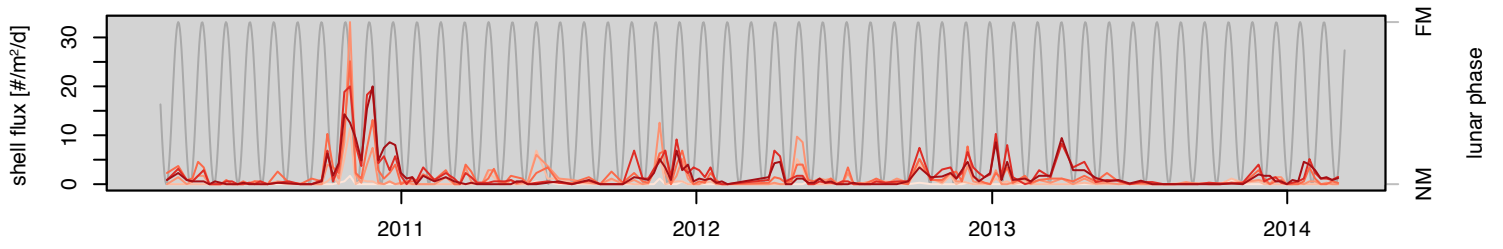
Table 1: ratio of square root of the power at the lunar and annual frequencies as a measure to compare the variance of the two cycles.

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

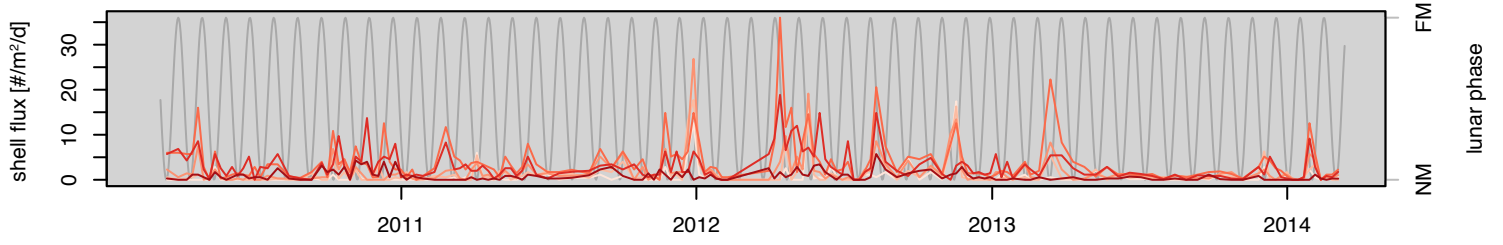
\* no clear annual cycle.



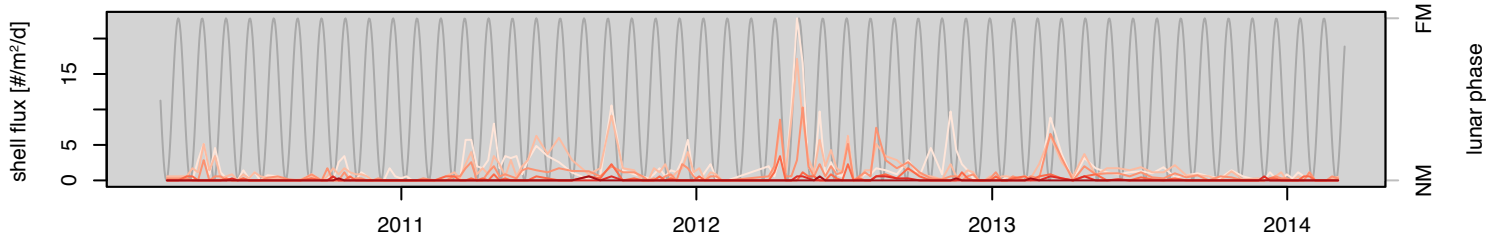
*G. menardii*



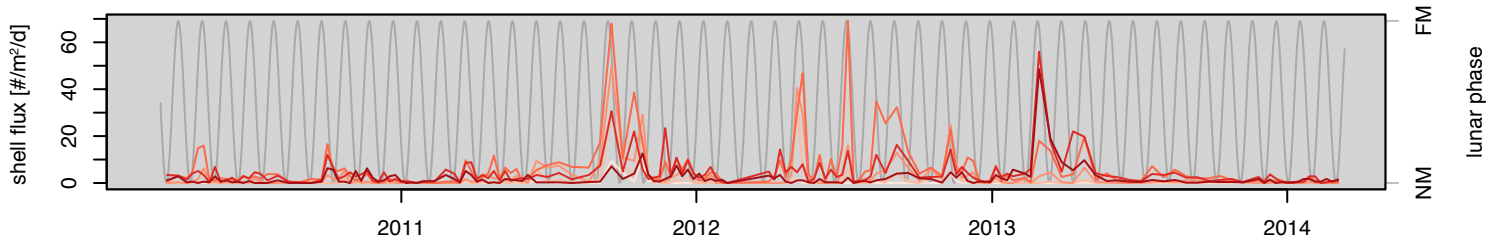
*G. siphonifera*



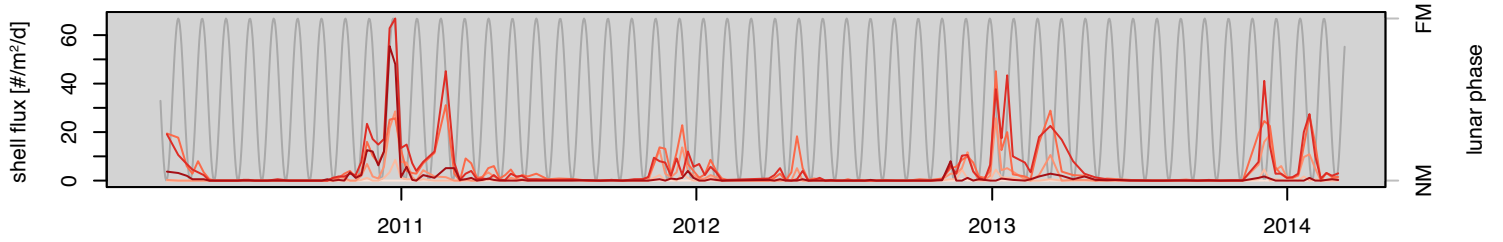
*O. universa*



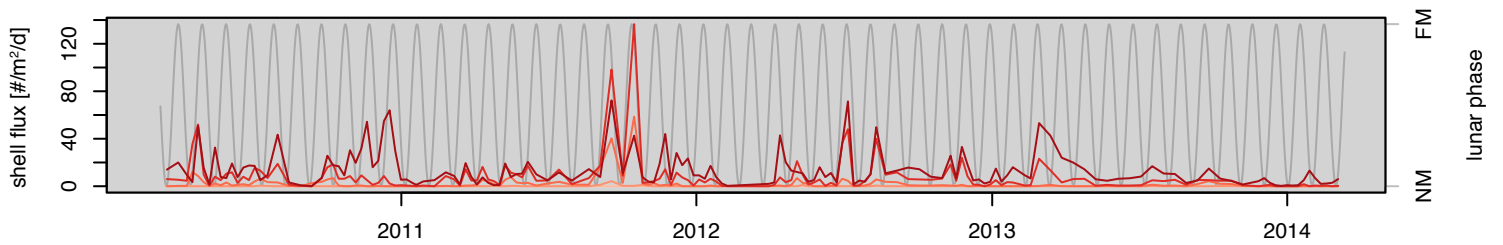
*G. sacculifer*



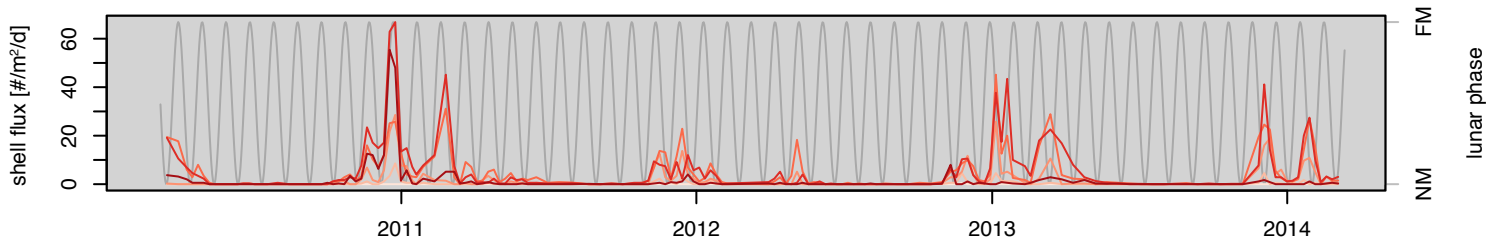
*G. ruber* (pink)



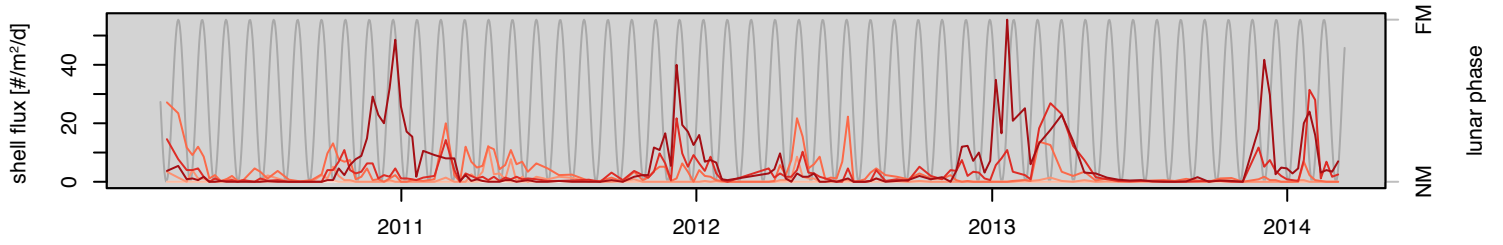
*G. ruber* (white)



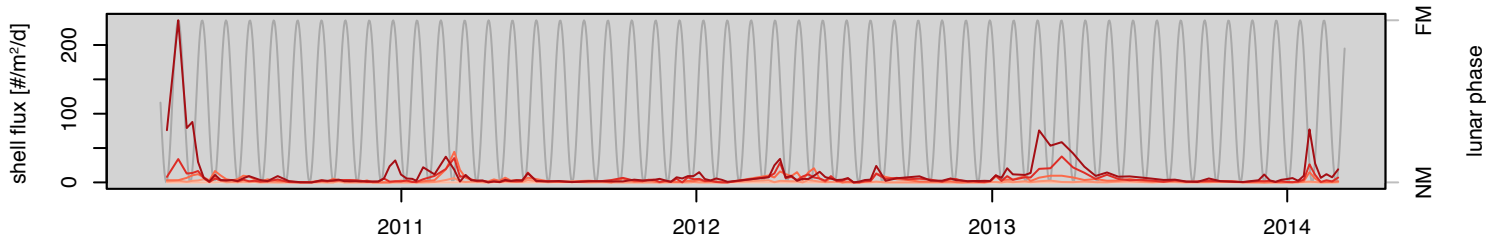
*P. obliquiloculata*



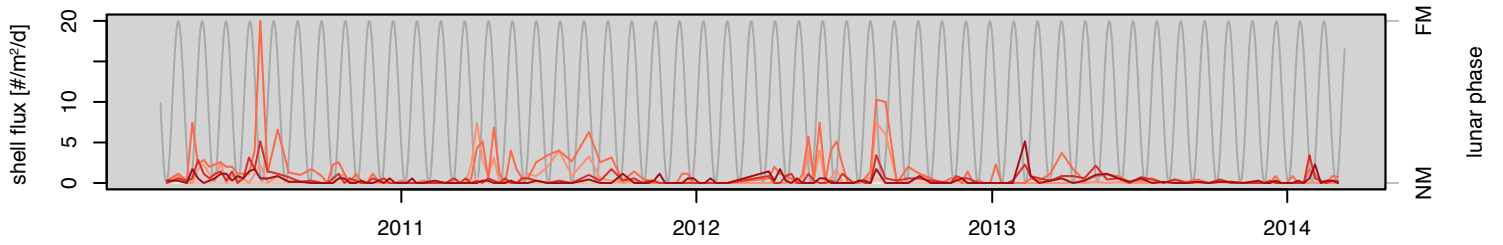
*N. dutertrei*



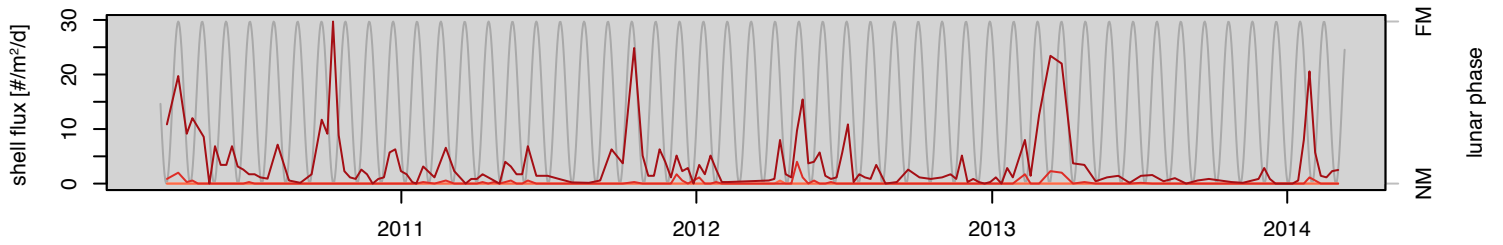
*G. calida*



*G. crassaformis*

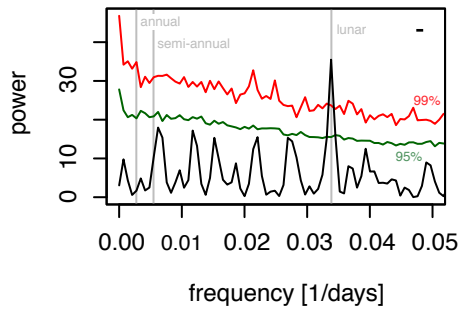


*G. glutinata*

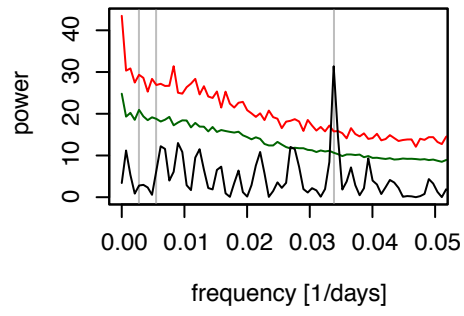


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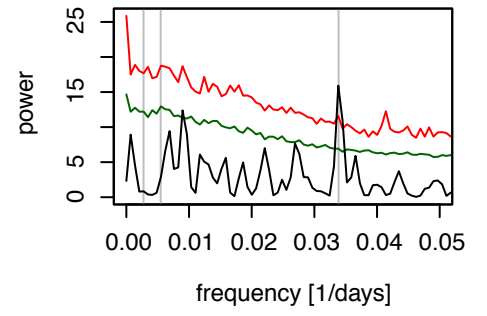
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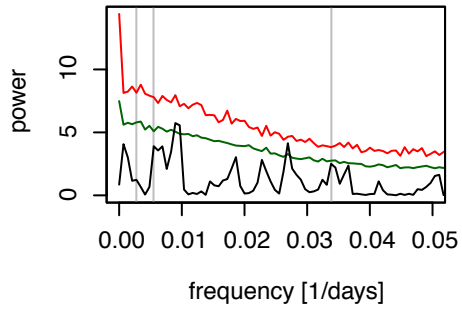
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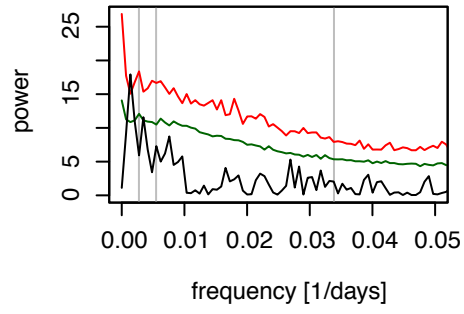
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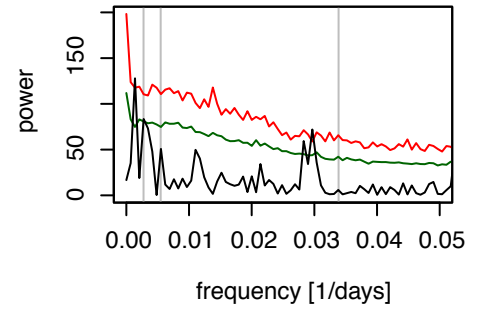
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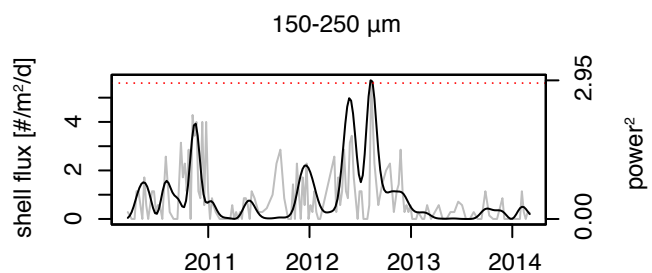
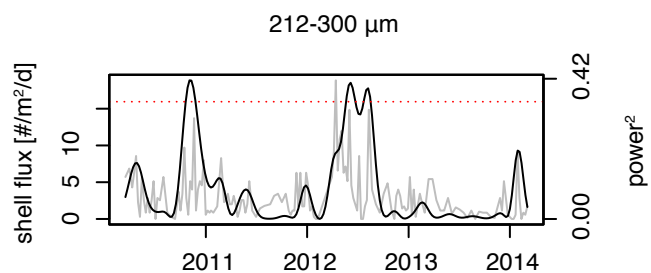
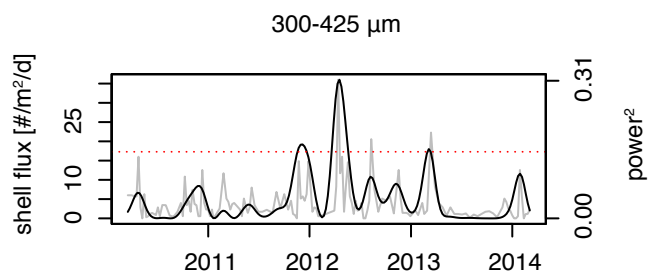
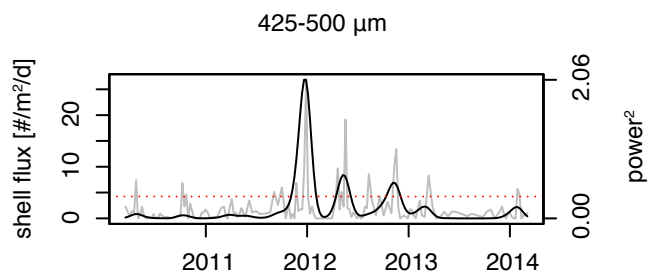
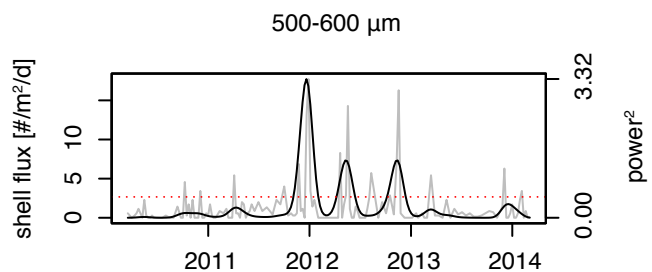
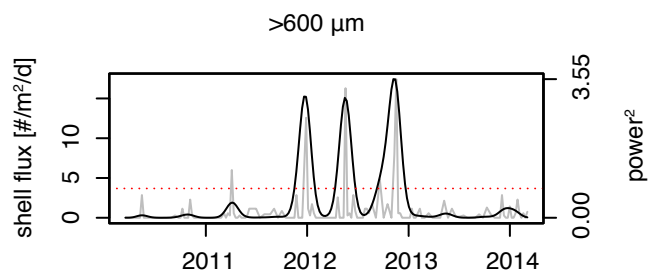


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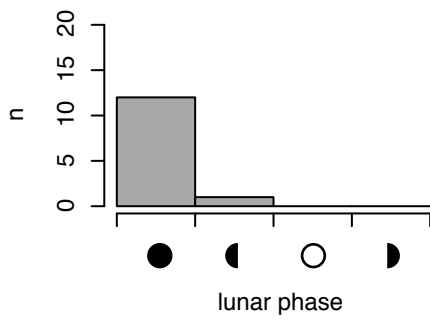


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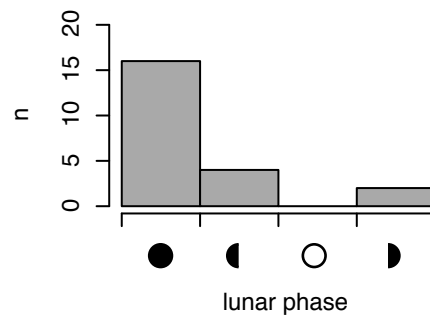




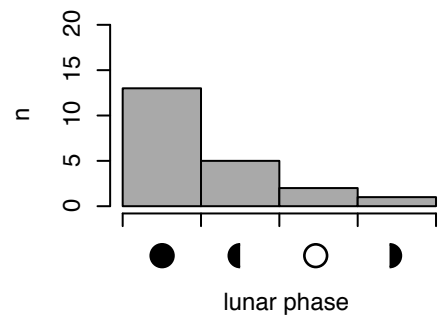
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500-600  $\mu\text{m}$



425-500  $\mu\text{m}$



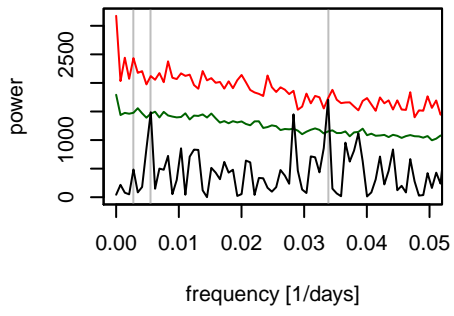
**Figure captions:**

S1 (page 3-13): periodograms of the size-fractionated fluxes of 11 species of planktonic Foraminifera in the Gulf of Mexico. See Fig. 2 for more details.

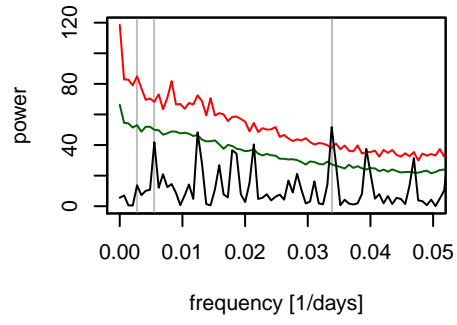
S2 (page 14-24): temporal expression of lunar periodicity in the shell flux of 11 species of planktonic Foraminifera in the Gulf of Mexico. See Fig. 3 for more details.

S3 (page 25-26): phasing of the lunar cycle in the shell fluxes of 11 species of planktonic Foraminifera in the Gulf of Mexico. Only size fractions that showed significant spectral power at the lunar frequency are shown. See Fig. 4 for more details.

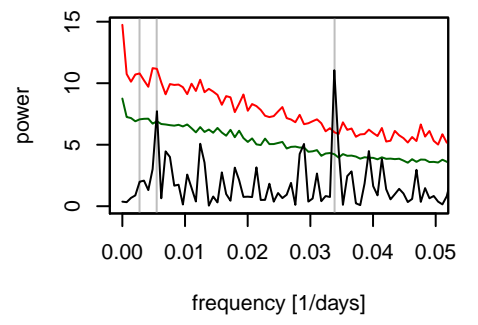
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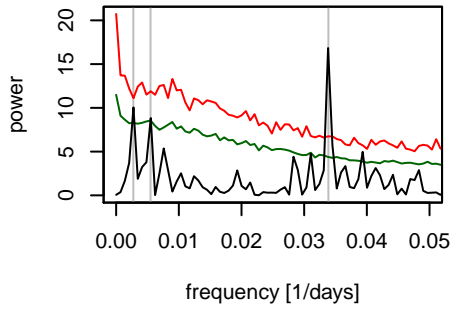
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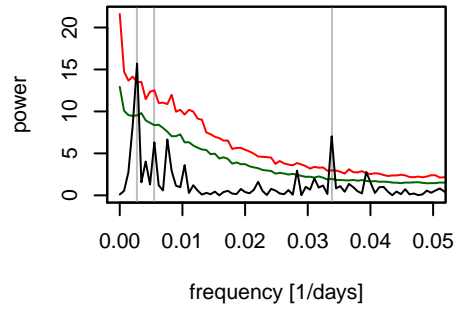
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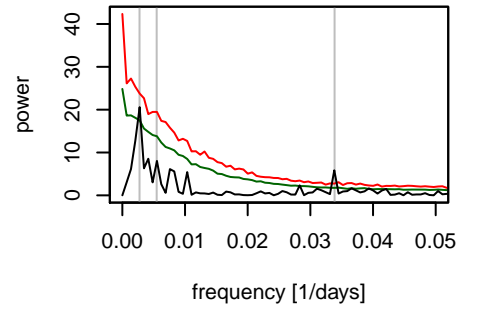
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*G\_men212*

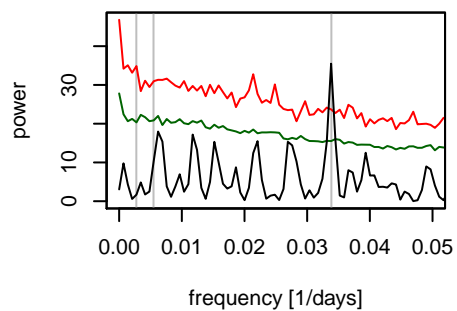


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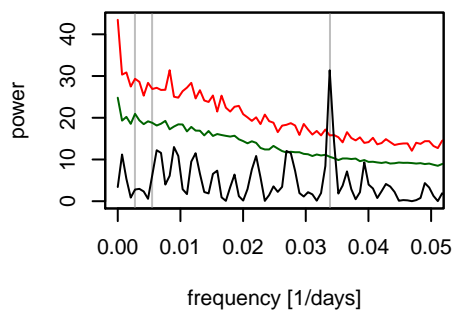




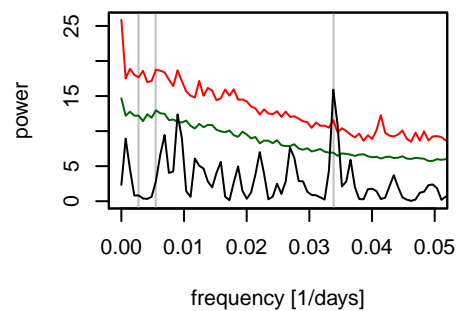
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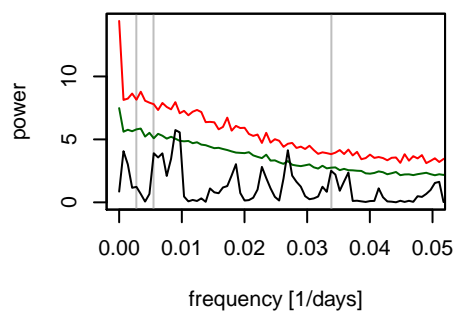
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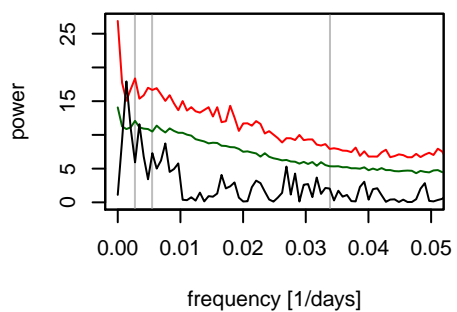
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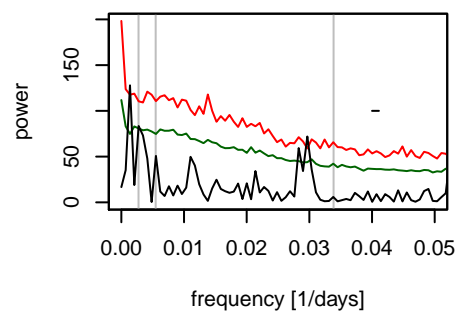
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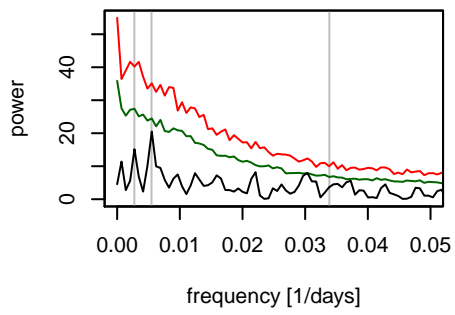
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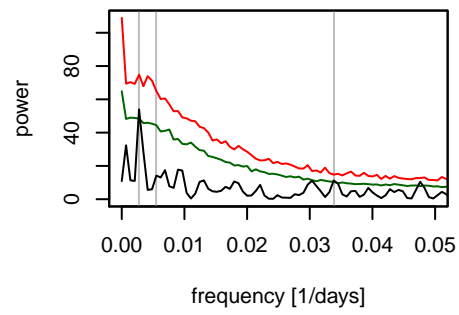
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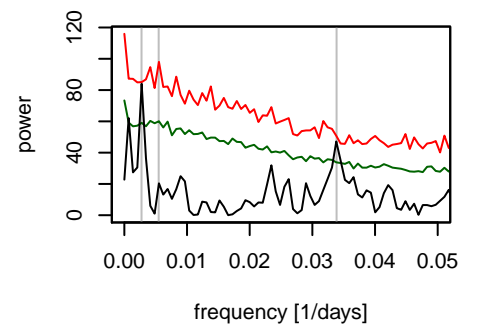
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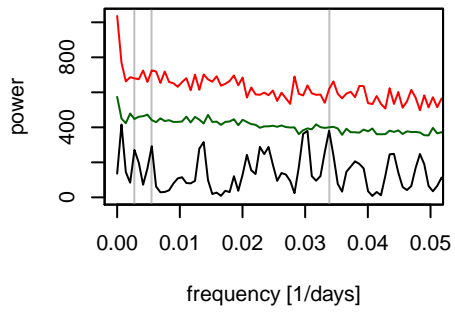
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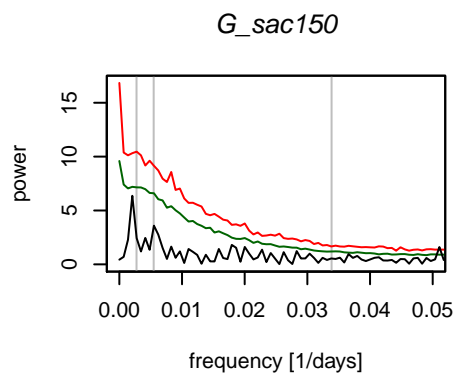
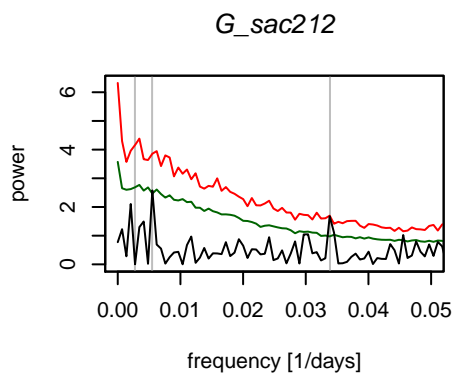
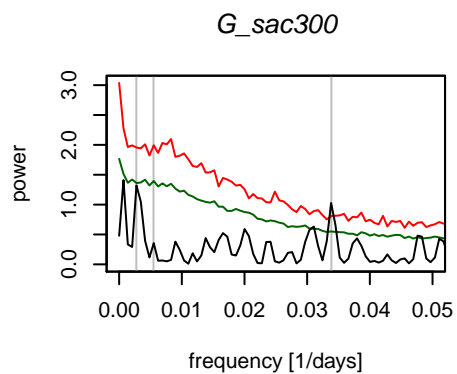
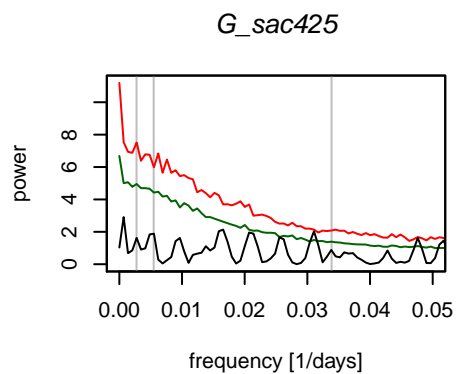
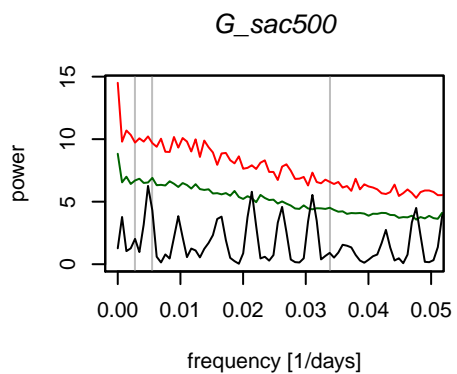
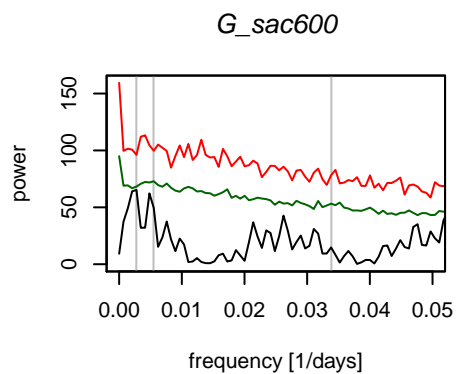


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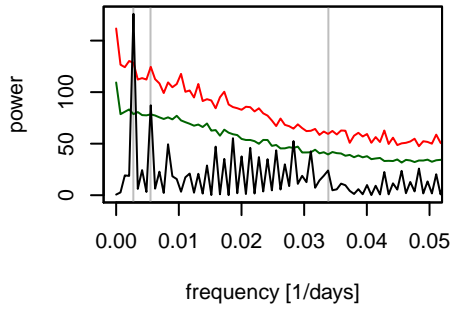


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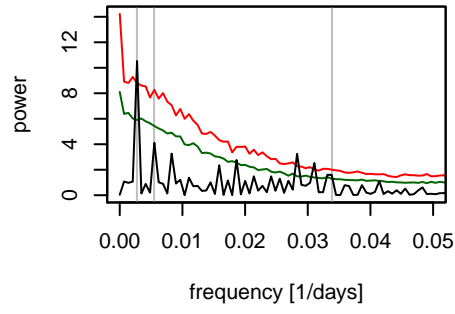




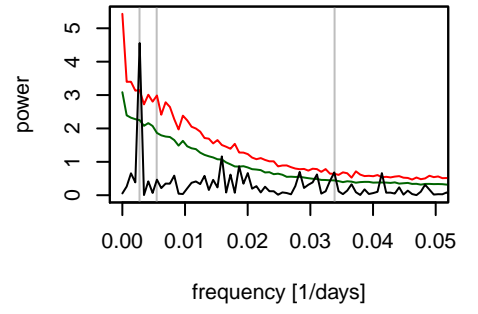
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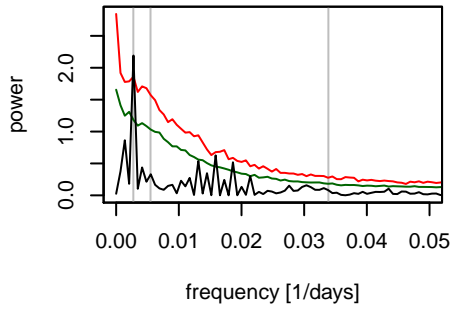
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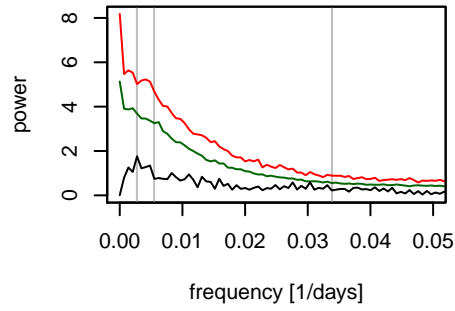
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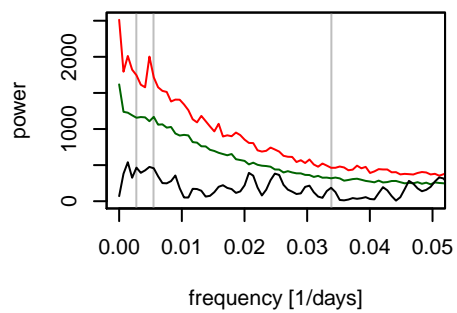
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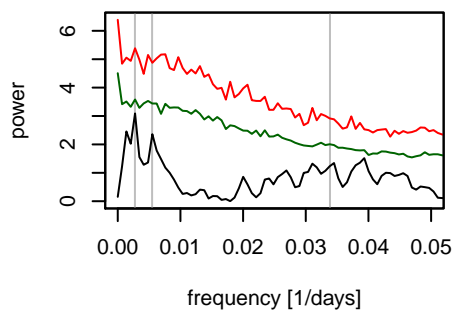
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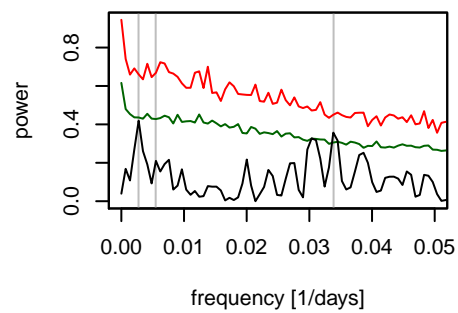
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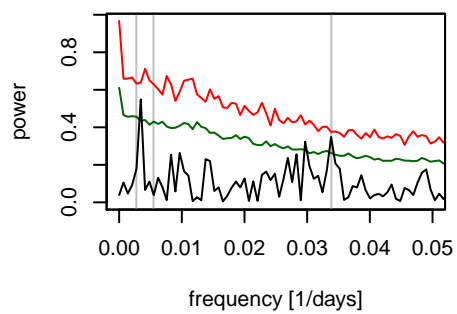
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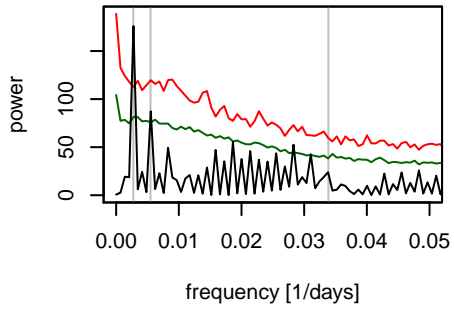
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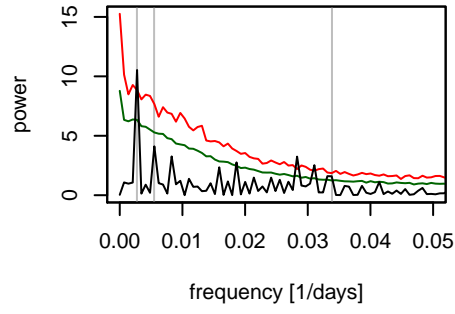
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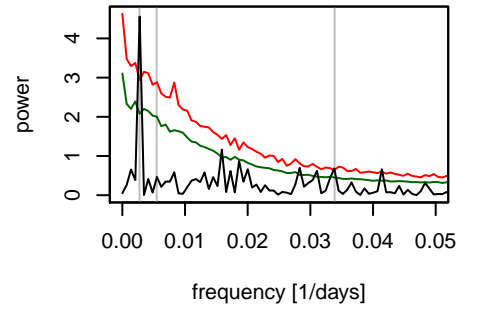
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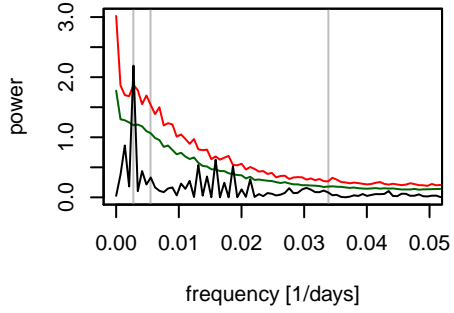
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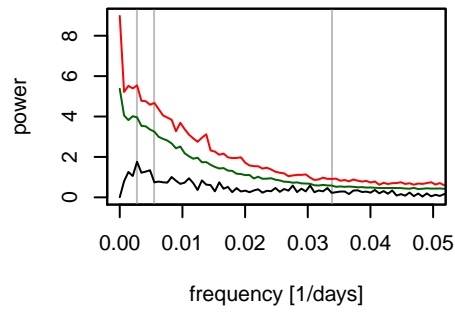
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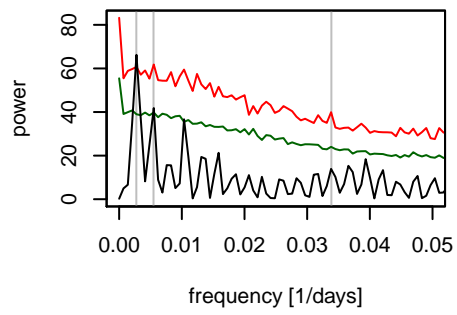
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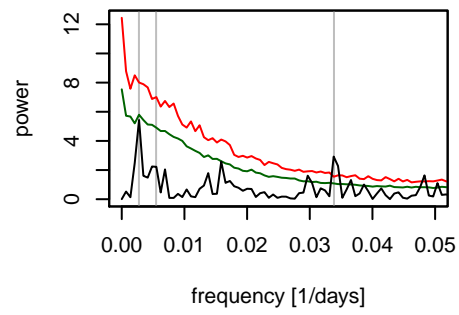
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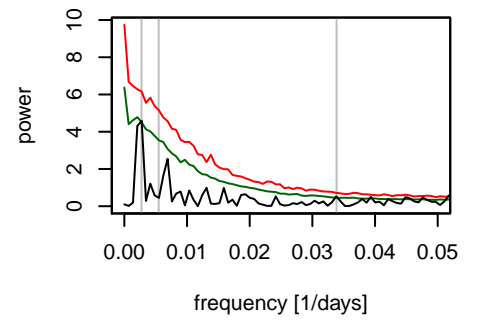
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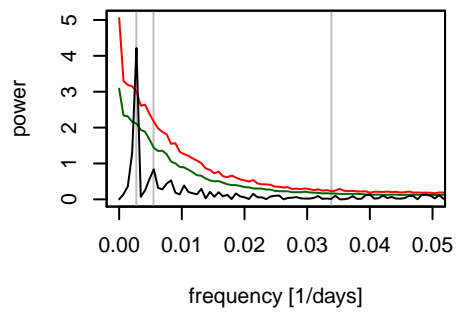
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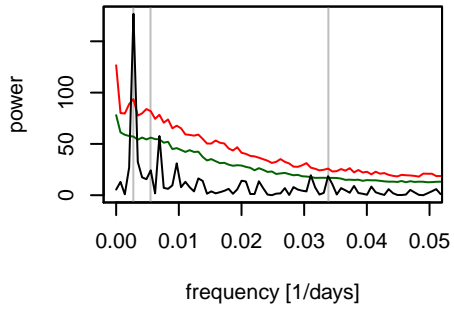
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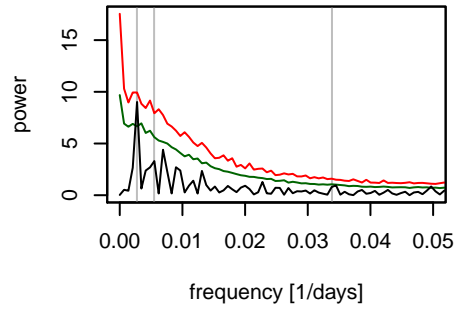
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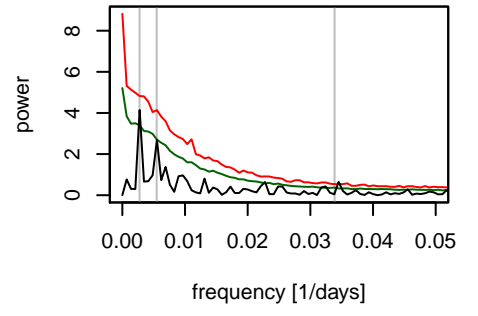
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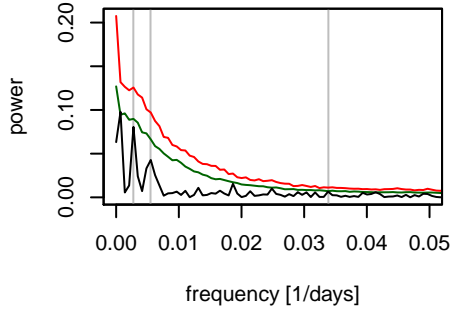
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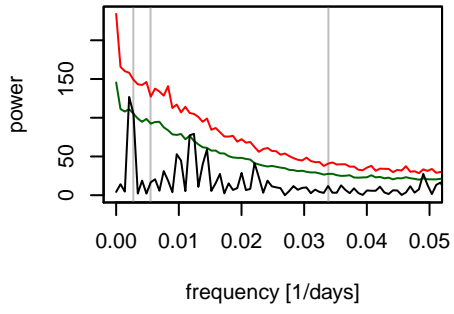


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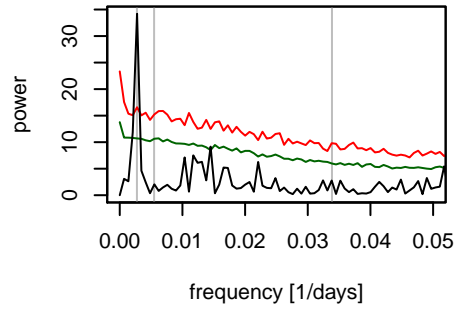




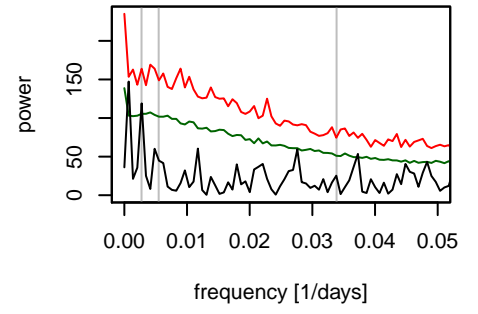
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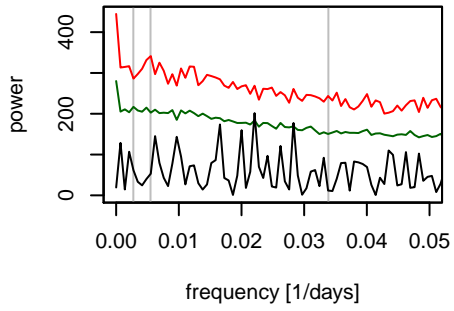
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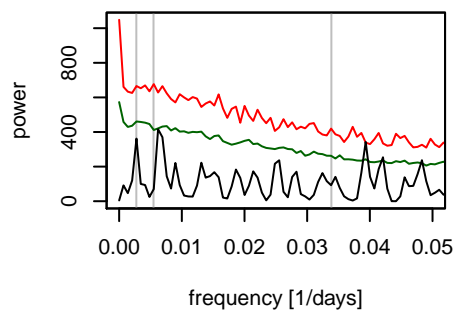
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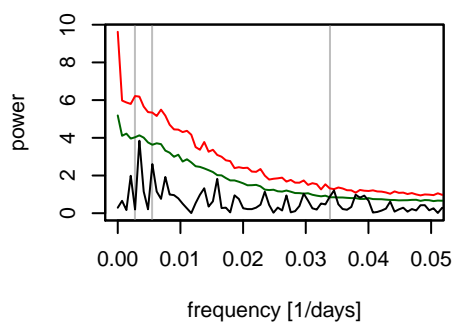
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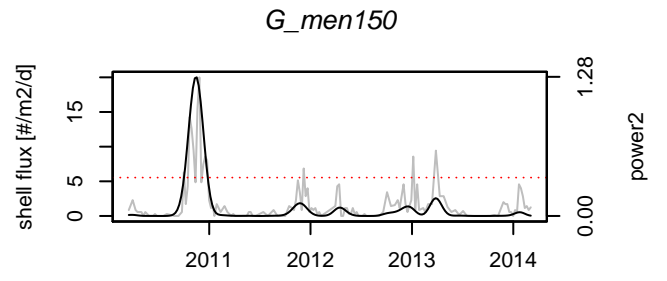
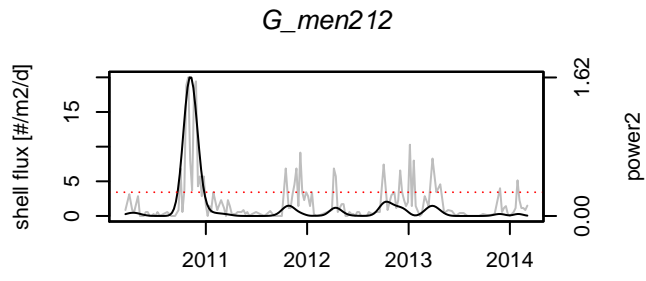
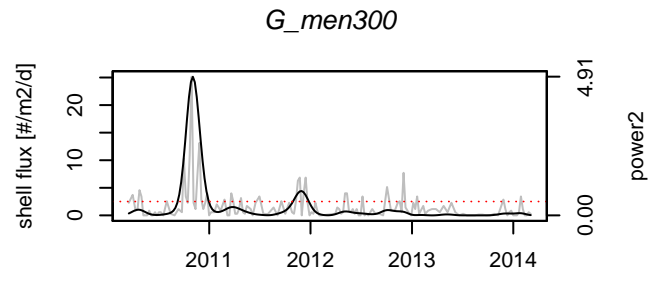
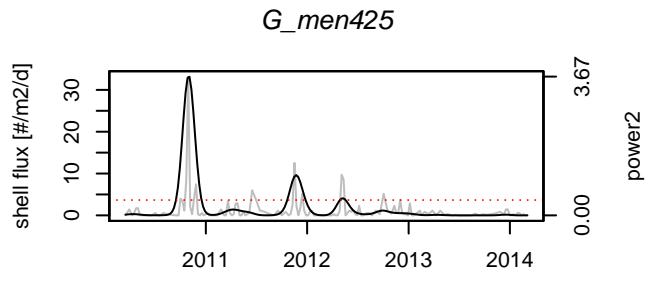
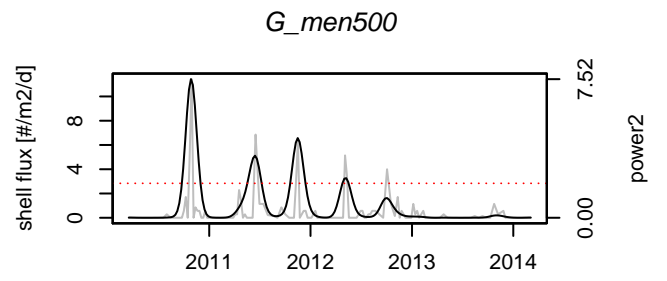
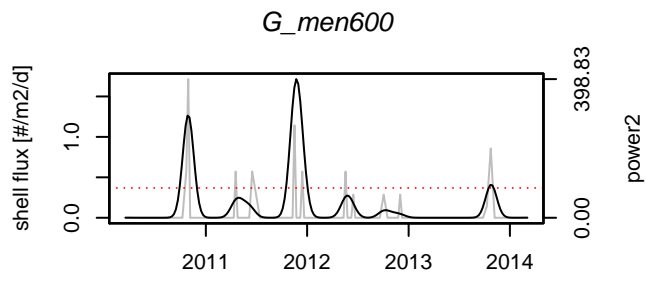


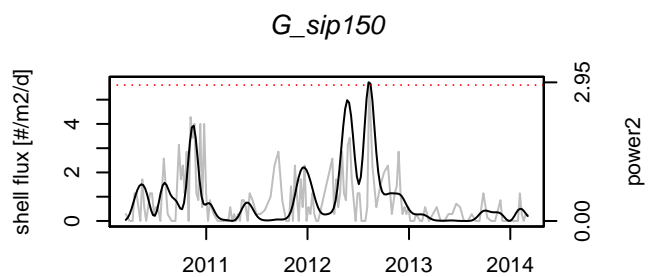
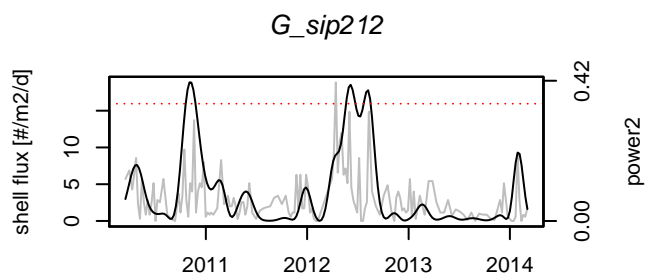
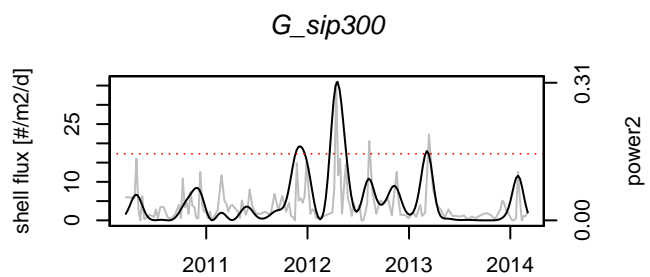
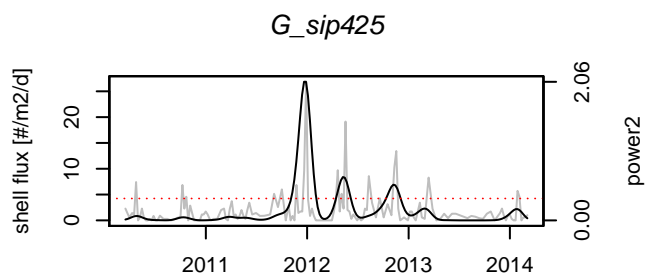
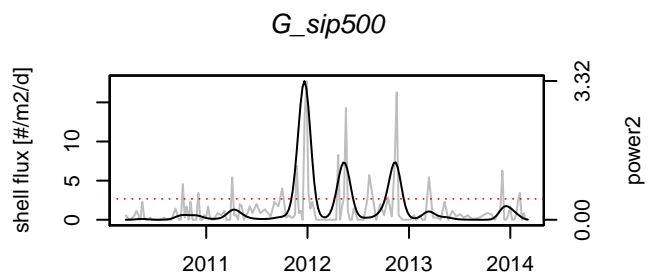
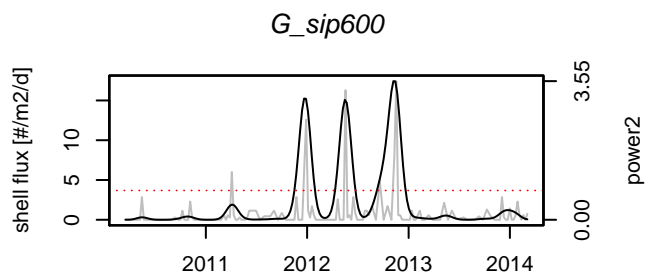
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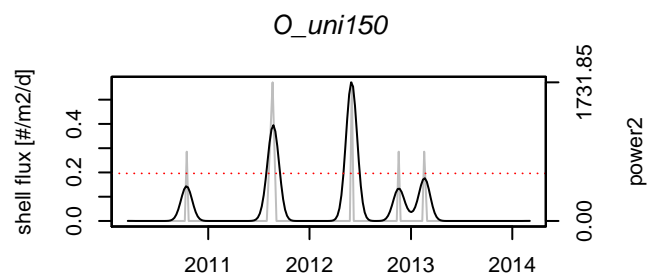
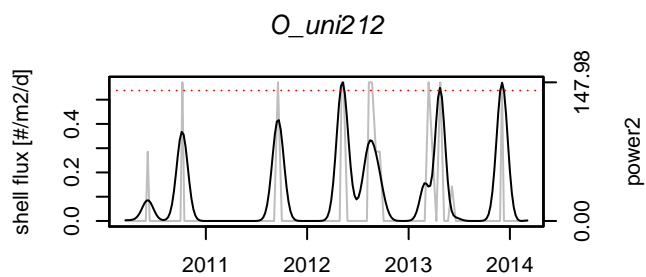
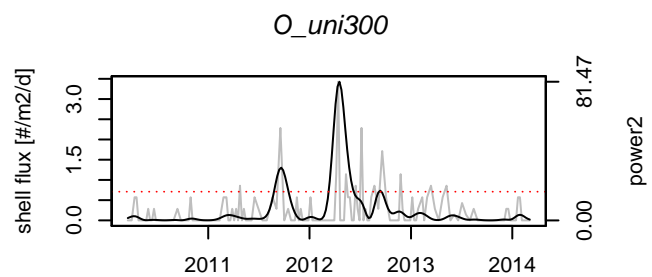
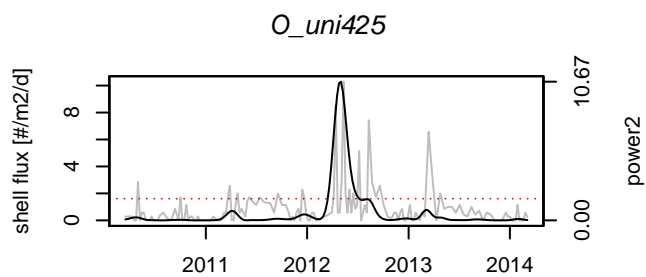
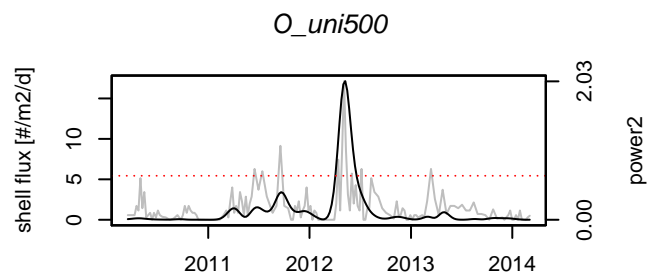
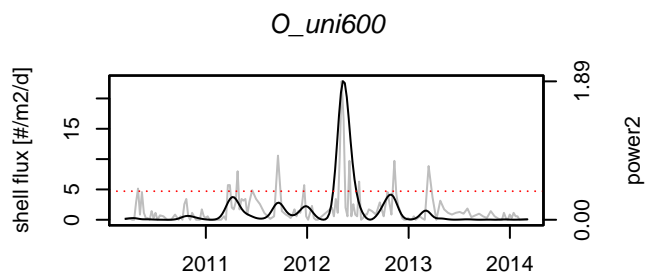


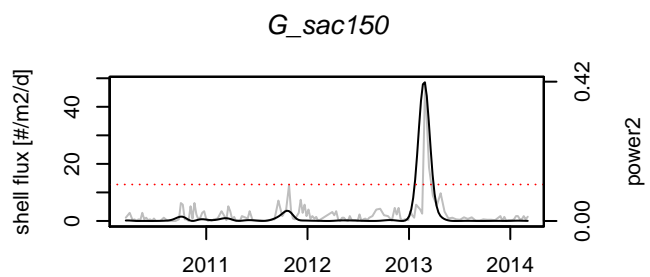
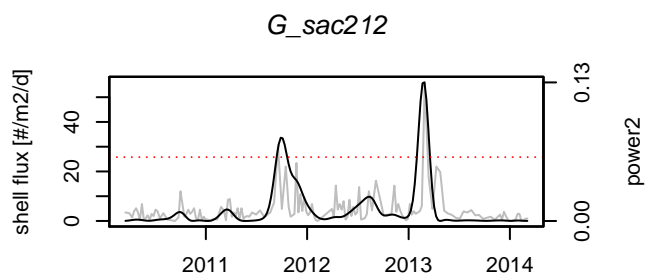
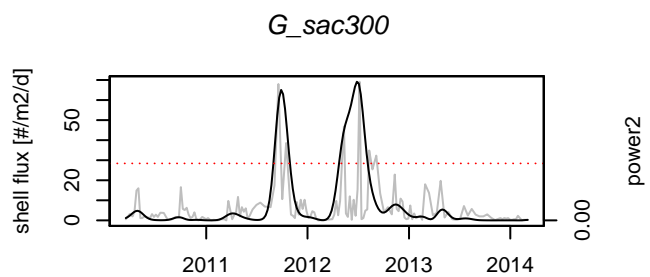
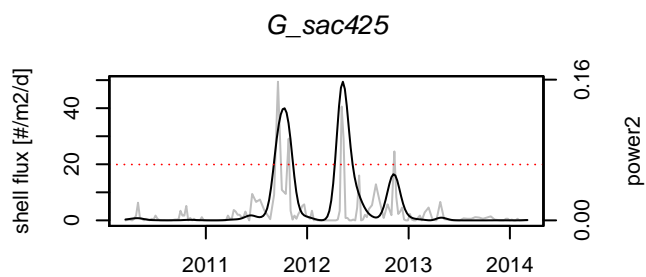
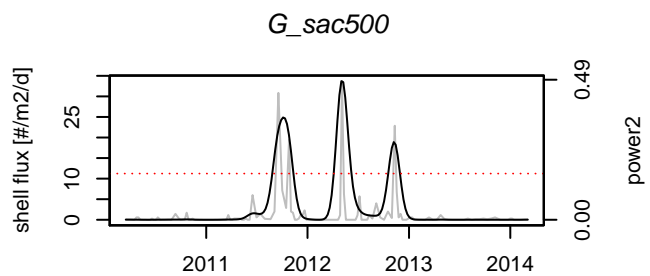
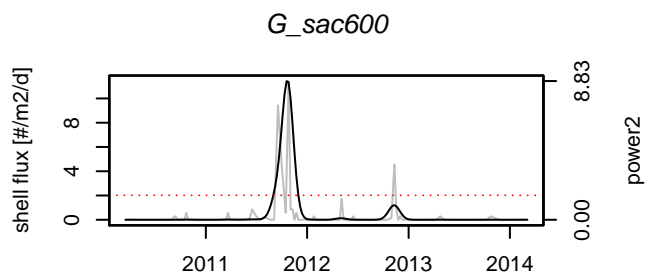
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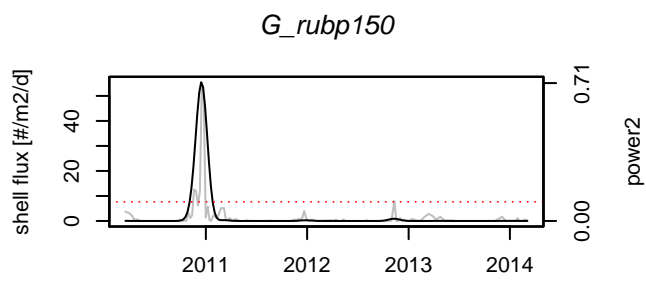
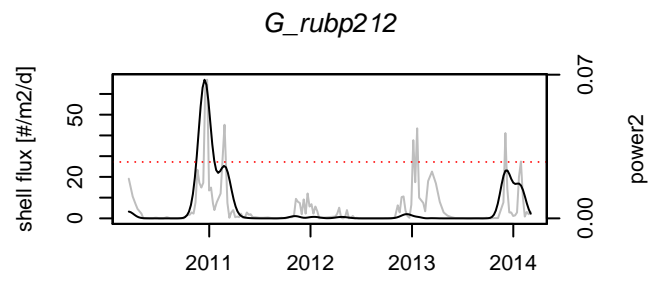
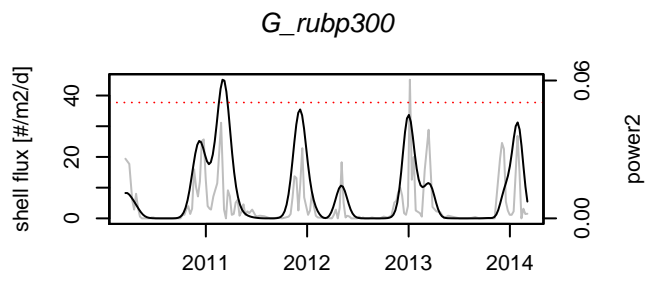
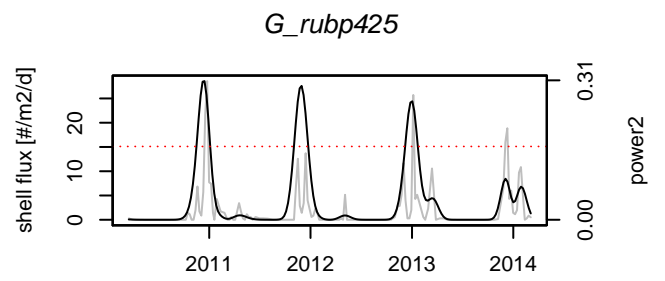
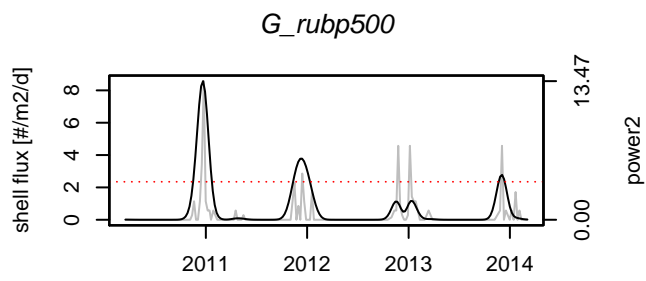


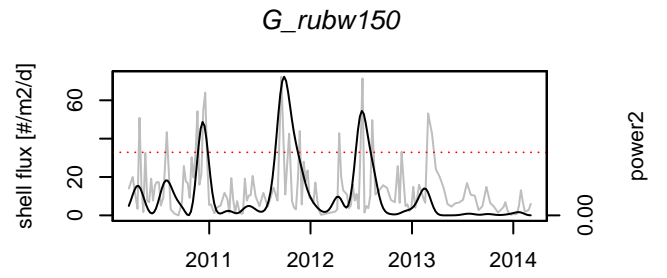
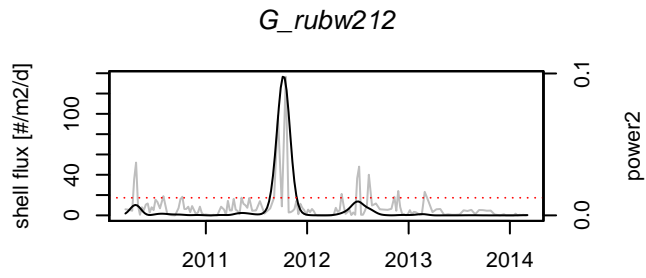
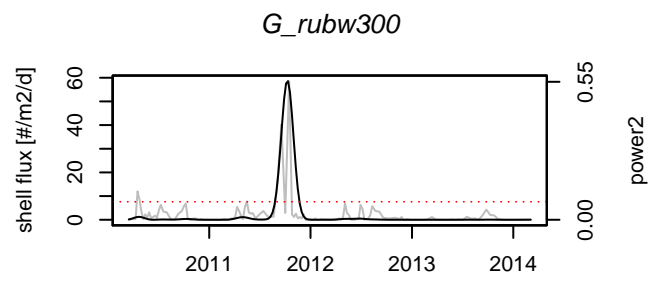
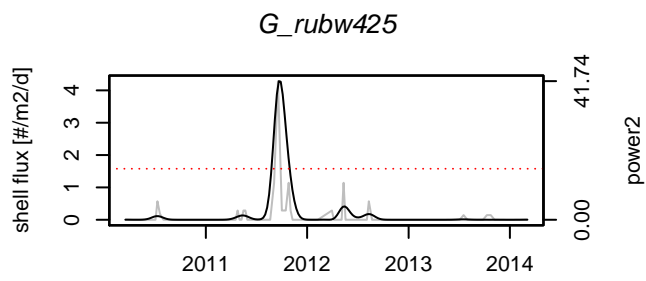




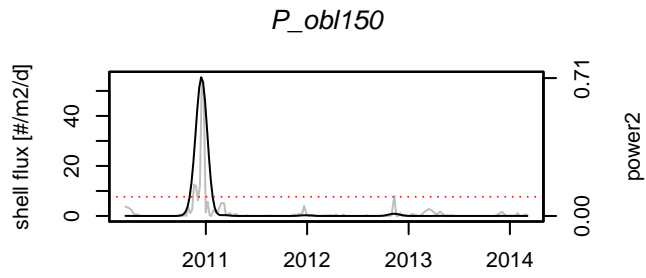
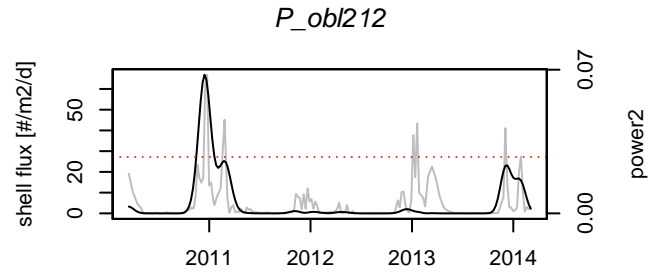
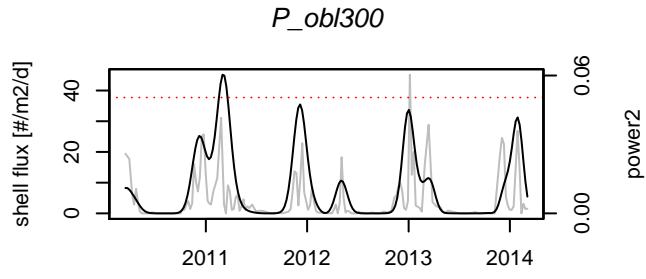
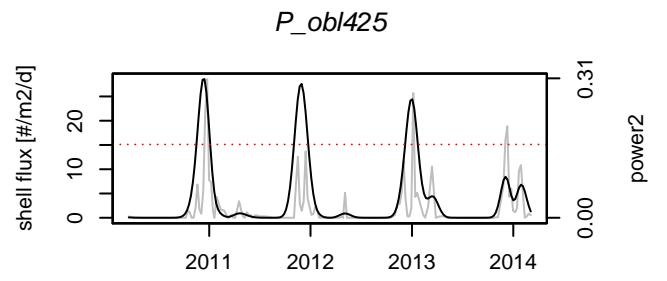
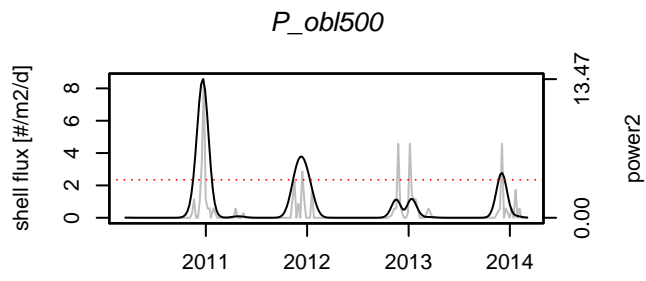


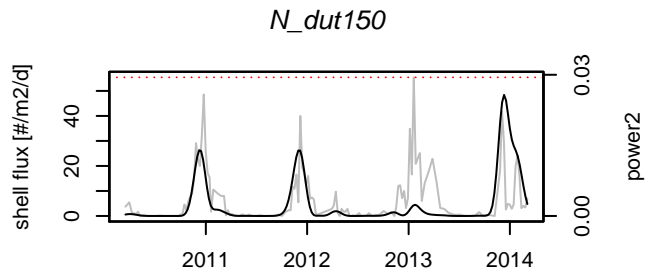
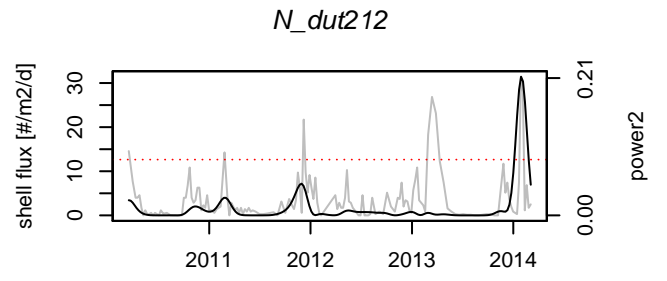
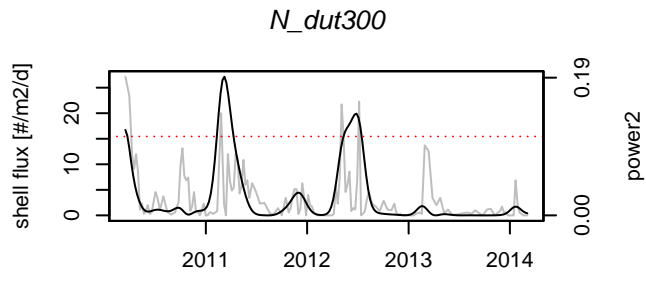
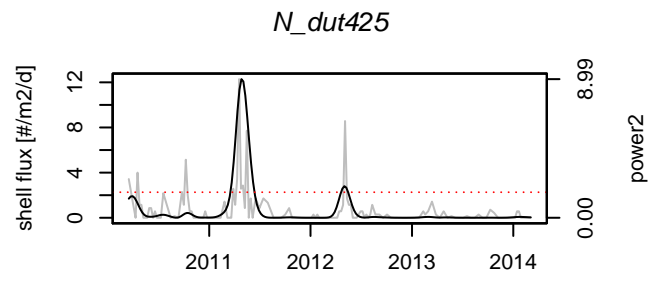
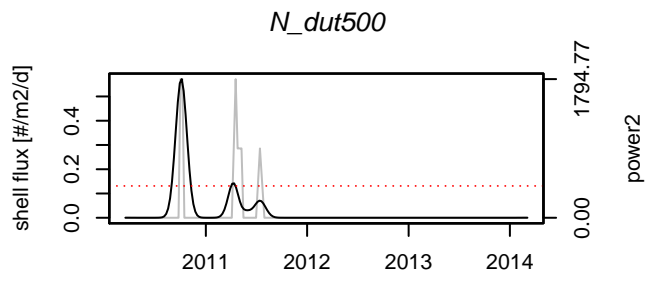


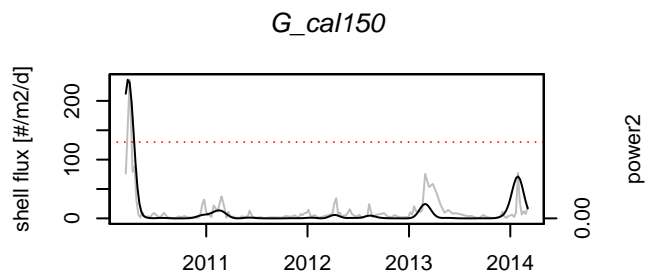
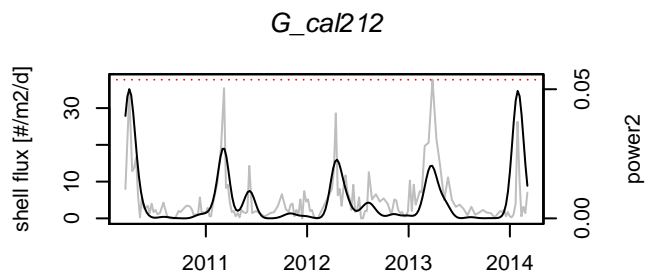
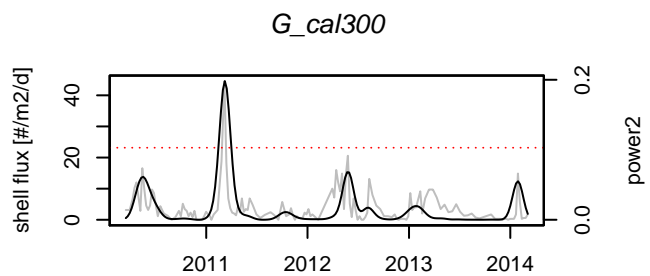
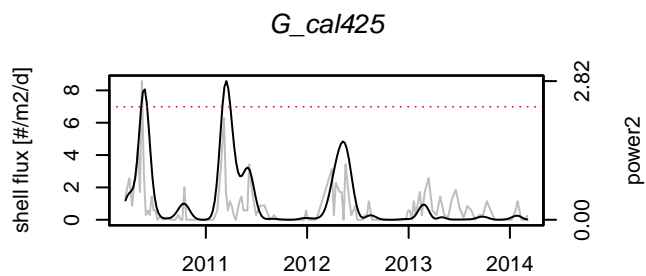


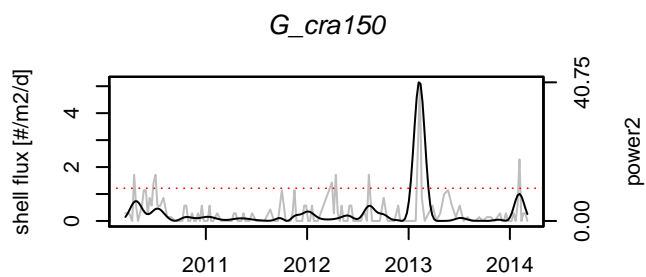
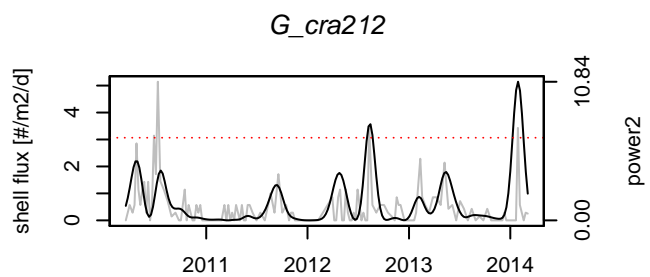
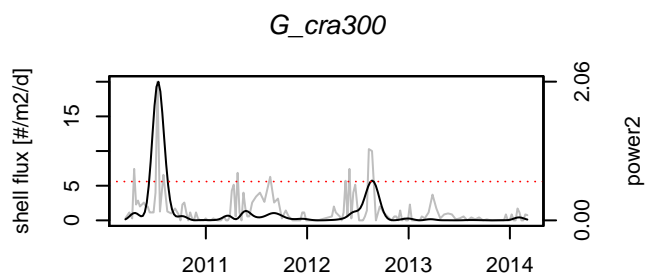
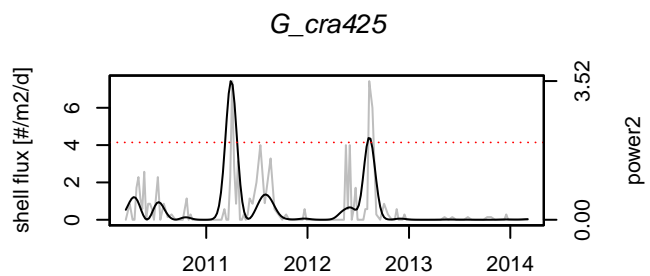
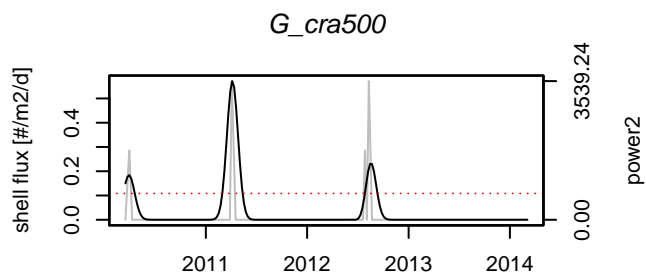


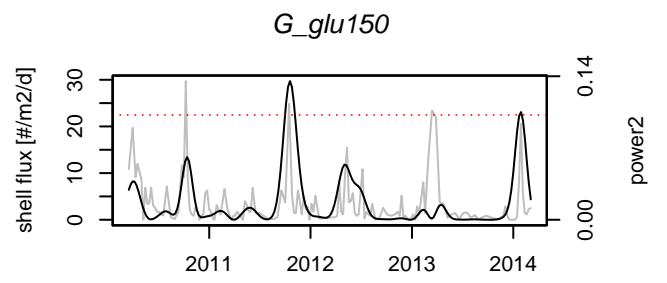
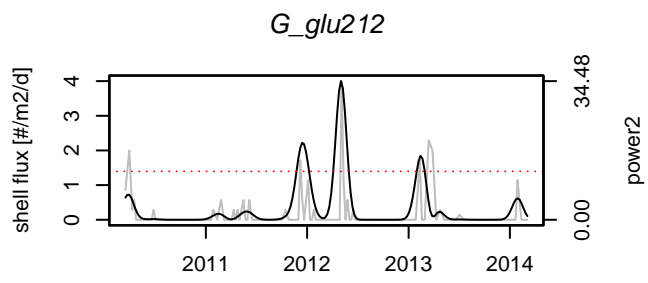




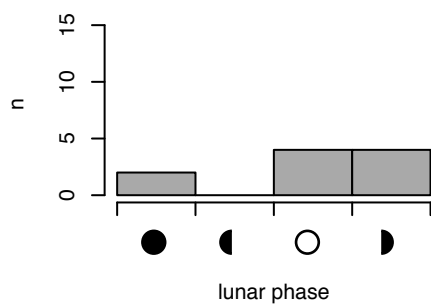




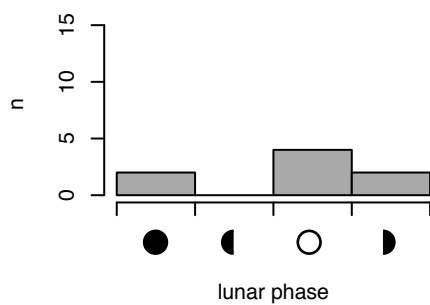




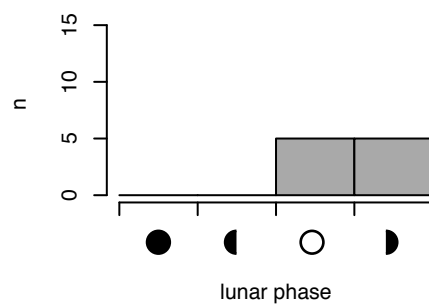
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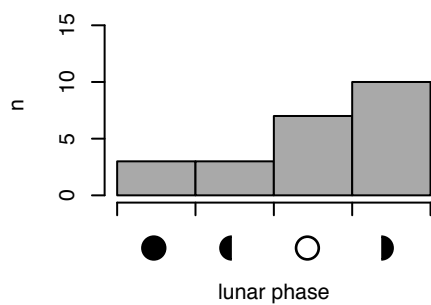
*G\_men500*



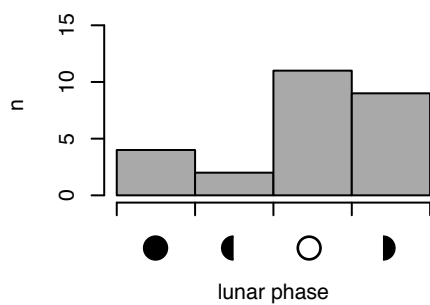
*G\_men425*



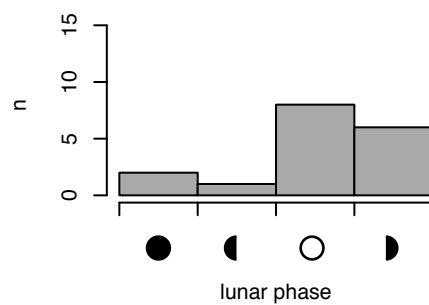
*G\_men300*



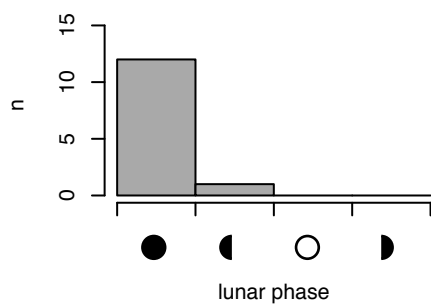
*G\_men212*



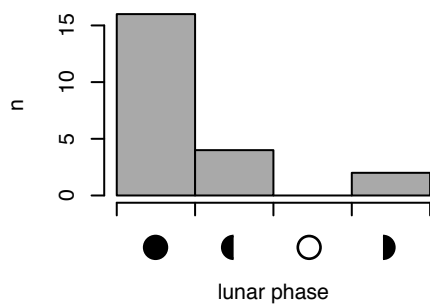
*G\_men150*



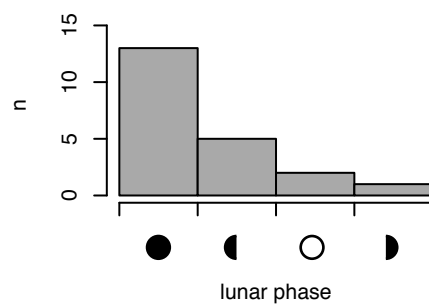
*G\_sip600*



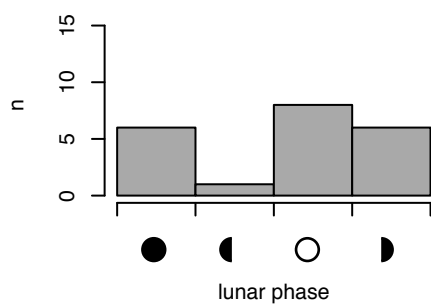
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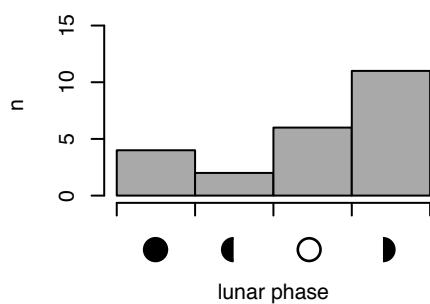
*G\_sip425*



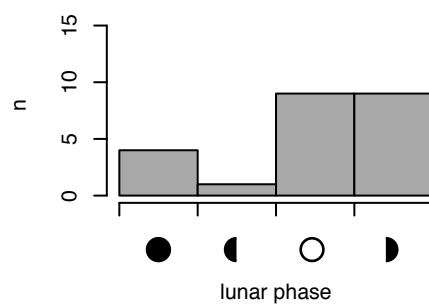
*O\_uni500*



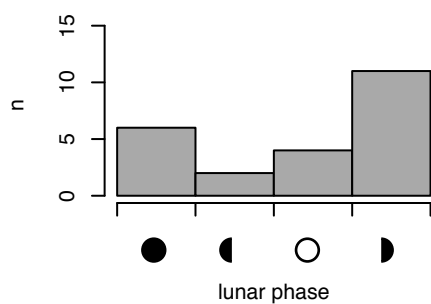
*O\_uni425*



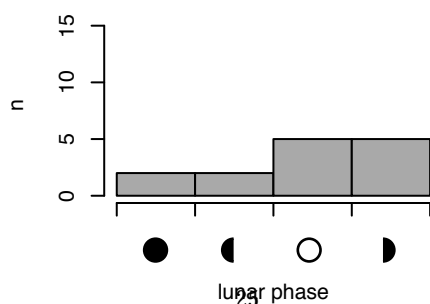
*G\_sac300*



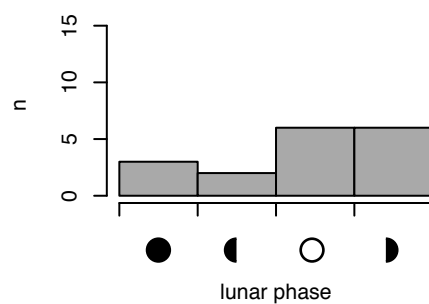
*G\_sac212*



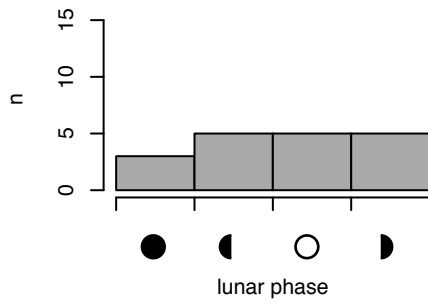
*G\_rubp425*



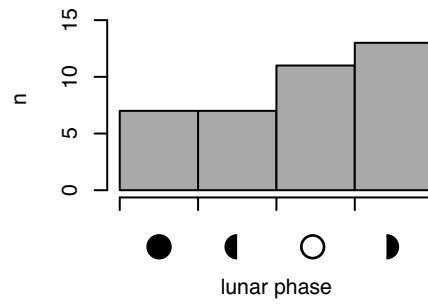
*G\_rubp300*



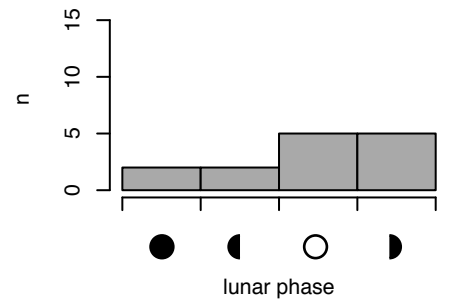
*G\_rubw212*



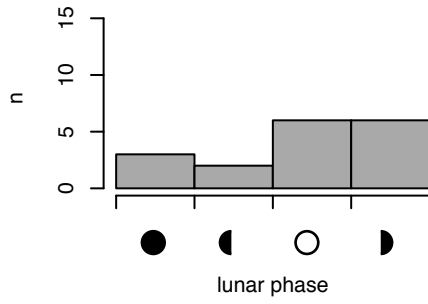
*G\_rubw150*



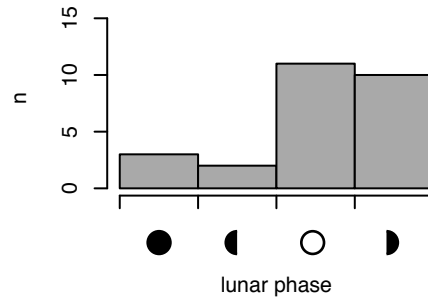
*P\_obl425*



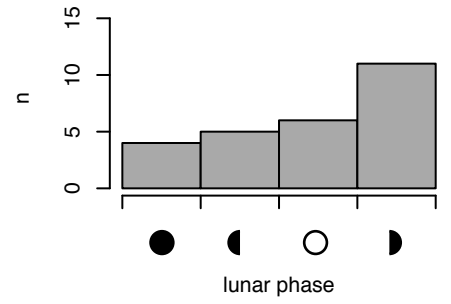
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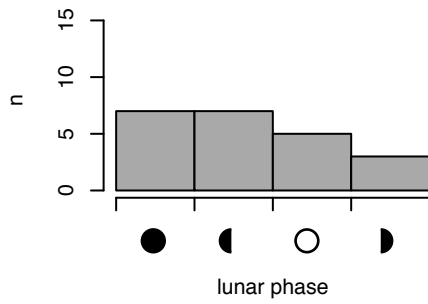
*N\_dut300*



*N\_dut212*



*G\_cal425*



*G\_glu150*

