

Planktonic foraminifera shell fluxes from a weekly resolved sediment trap record in the southwestern Atlantic: Evidence for synchronized reproduction

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ABSTRACT

The reproductive behavior of planktonic foraminifera is an important variable for the interpretation of paleoproxies based on their shells and for the understanding of the role of these organisms in oceanic carbonate flux. Observations from plankton tows have initially provided evidence for the existence of reproductive cycles synchronized with lunar phases in several species. However, subsequent observations from sediment traps yielded inconclusive results. Here we report shell flux data of four key species of planktonic foraminifera (*Trilobatus sacculifer*, *Globigerinoides ruber*, *Orbulina universa* and *Neogloboquadrina dutertrei*) from multiple deployments of a high-resolution (3–7 days) sediment trap in the southwestern Atlantic. Despite the potential bias related to lateral advection at the shallow deployment depths of the traps, the unusually high sampling resolution makes it possible to better constrain the short-term (lunar) dynamics of shell flux than most previous studies. Using periodic regression on the high-resolution series, we detected for all species evidence for a single flux maximum during one lunar cycle, occurring approximately 4–6 days after the full moon. In this series, 44–52 % of the shell flux in the deep (100 m) trap occurred during the last quarter. Different flux behavior between the shallow (50 m) and the deep (100 m) traps co-located on the same mooring revealed evidence for migration to deeper levels prior to reproduction in *T. sacculifer*. Although a monthly peak in shell flux was observed in the 3-day resolution deployment, its signature disappeared when all deployments were analyzed together. This analysis still reveals an elevated flux during the last quarter of the lunar cycle, but it seems that the period of the reproductive cycle is not fixed in time. Combined with aliasing at the sampling resolution of 5–7 days, this variable timing overwhelms the strictly periodic component of the shell flux series. We conclude that planktonic foraminifera shell flux and thus the carbonate export to the seafloor is affected by periodicity in the lunar band, but that reproduction does not seem to occur at exactly the same day of the lunar cycle in each month.

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1. Introduction

Synchronized reproduction seems to be a common feature in many marine organisms. For instance, reproductive cycles in reef corals (Zakai et al., 2006) and crustaceans (Skov et al., 2005) were pointed out to be synchronized with the moon phases. These lunar-driven reproductive cycles can be interpreted as an evolutionary adaptation to enhance the probability of gamete union in gamete-broadcasting species (Spindler et al., 1979). Based on observations from the plankton, such a reproductive strategy has also been suggested for several species

of planktonic foraminifera (Spindler et al., 1979; Hemleben et al., 1989; Bijma et al., 1990a). If the periodicity in planktonic foraminiferal reproduction is strong, it would affect the temporal pattern of carbonate flux to the seafloor. Since planktonic foraminifera are major contributors to the oceanic carbonate flux (Schiebel, 2002), investigations of the role of their reproductive cycles are needed to better constrain the role of foraminifera shell fluxes in oceanic carbon cycling and particle ballasting.

Laboratory experiments with *Hastigerina pelagica* showed that this species follows an endogenous lunar reproductive cycle (Spindler et al., 1979). Subsequent studies using plankton tows in the Red Sea demonstrated that lunar reproductive synchronization might also be present in other foraminifera species such as *Trilobatus sacculifer*, with a full synodic lunar cycle, and *Globigerinoides ruber* and *Globigerinella siphonifera*, which were associated with a semi-lunar cyclicity (Bijma

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et al., 1990a, 1994; Erez et al., 1991). The study of Bijma et al. (1994) demonstrated that *T. sacculifer* fluxes are characterized by pulses instead of a constant particle rain and pointed to the relevance of this reproductive behavior for predictions of the carbonate flux. These observations support the theory of a synchronous reproduction in planktonic foraminifera, which would be an advantage for these organisms that reproduce by gamete broadcasting.

In contrast to plankton tows, which only provide snapshots of population dynamics in time and space, sediment trap data should in theory be more suitable to assess foraminifera reproductive cycles through temporal variations in their shell fluxes (Kawahata et al., 2002; Zaric et al., 2005; Rigual-Hernández et al., 2012). Provided they are sampling at sufficient temporal resolution, sediment traps have the potential to provide time series of foraminiferal fluxes, from which periodic cycles in the lunar band could be detected (Khrapounoff et al., 1998; Lončarić et al., 2005; Kuroyanagi et al., 2008). Unfortunately, the resolution of sediment trap series is usually too low for the detection of lunar cycles. Most sediment trap studies use variable temporal resolution depending on the season (King and Howard, 2001) and have long periods with a bi-weekly sampling, which hampers the detection of cycles in the lunar band.

So far, there are only a few sediment trap series published that could provide meaningful insights into short timescales. A 12 to 15-day resolution study Kawahata et al. (2002) inferred the existence of a lunar reproduction cycle for *T. sacculifer* in the North of New Guinea. However, their resolution was too low and the cycle could only be evidenced during a short period of the entire time series. Lončarić et al. (2005) analyzed shell flux data for 28 planktonic foraminifera species in the South Atlantic (8 days sampling configuration, comprising 7-month sampling collection). These authors were able to infer a ~29.5 days synodic lunar cycle, but only for *H. pelagica*, whereas all other species did not seem to follow this pattern. A recent study of Lin (2014) off southwest Taiwan, with an outstanding resolution of 3 days, detected a probable influence of lunar reproduction on *T. sacculifer* and *G. ruber* fluxes. However, despite the combined analysis of flux data and shell sizes, the relationship between lunar phase and reproduction was not always present throughout the 3-months sampling interval. Finally, Jonkers et al. (2015) analyzed the flux variability of 11 species in a long sediment trap series from the Gulf of Mexico with a resolution of 9 days. These authors could detect lunar periodicity in all investigated species, but the lunar rhythm was not present in all size fractions.

Summarizing, it seems that foraminiferal fluxes are episodic on the time scale of weeks and the flux pattern is consistent with reproduction synchronized around the lunar band, but the lack of a clear signal in many studies (Kawahata et al., 2002; Lončarić et al., 2005) is puzzling. It is also unclear why the lunar cycle is not observed in all species investigated (Lončarić et al., 2005; Jonkers et al., 2015) and to what degree the postulated relationship with a specific lunar phase is universally applicable. Sediment trap studies alternatively indicate reproduction before full moon (Lin, 2014), shortly after (Lončarić et al., 2005), or at full moon (Kawahata et al., 2002). Recently, Jonkers et al. (2015) found highest fluxes around full moon for a group of species (*Globorotalia menardii*, *Orbulina universa*, *Trilobatus sacculifer*, *Pulleniatina obliquiloculata*, *Neogloboquadrina dutertrei*, *Globigerinella calida* and *Globigerinita glutinata*), and around the new moon for *G. siphonifera* and *G. calida* at the same location.

In this study, we aim to investigate short-term dynamics in the vertical flux variability of planktonic foraminifera using sediment trap samples from a mooring at the Southeastern Brazilian continental shelf. This region harbors typical subtropical assemblages of planktonic foraminifera (Lessa et al., 2014) with many species for which lunar synchronization of reproduction has been postulated (Bijma et al., 1990a). In order to assess the possible periodicities in the shell fluxes records, we evaluated the vertical mean flux in a shallow and deep traps co-located on the same mooring and analyzed a 16-month foraminiferal mean flux datasets of four different species (*G. ruber*, *T. sacculifer*, *N.*

dutertrei and *O. universa*). Our time series is composed of an initial period with 36 days sampled at 3-day intervals and a longer subsequent period sampled with lower resolution (5–7 days). The duration of the full experiment covered approximately ten lunar cycles.

2. Materials and methods

2.1. Sediment trap sampling

The mooring line that was available for the study of reproductive synchronization was deployed within the Brazilian Project *Ressurgência*. The sediment traps at depths of 50 and 100 m, described as L = 50 or L = 100, are located on the Brazilian southeastern continental shelf at 23°36' S 041°34' W (Fig. 1), at a depth of 145 m. The used sediment traps PARFLUX (model Mark 8-13) have an aperture area of 0.25 m² and 13 sequential bottles with 500 ml capacity. Each sample bottle was decontaminated and filled with pre-filtered MilliQ water with buffered (pH = 8) formaldehyde (4%) after adjusting the salinity with marine salt (RedSea®) to 70 PSU to prevent mixing and bacterial decomposition of collected particles (Goswami, 2004). In addition to the traps, the mooring line contained temperature loggers (ONSET tidbits V2) between 30 m and 120 m, spaced at 5 m intervals and two current meters (400 kHz Nortek Aquadopp Profilers) configured for up and down looking acoustic current profiling. The physical parameters (temperature and velocities) were measured at 30-minute intervals. Current-meter data are provided as supplementary material (Appendices B and C). Albuquerque et al. (2014) recently published a general description of particle fluxes and bulk composition.

All samples and data used in this study were retrieved during four deployments between November 2010 and March 2012, resulting in time frames of 39 and 91 consecutive days. Sampling resolution was not identical for all deployments. The first experiment, from November 11th to December 19th 2010, had a 3 days sampling rate. The second experiment, from March 15th to June 14th 2011, had a 7 days sampling rate. The third experiment, from July 20th to September 26th 2011, had a 5 days sampling rate and the last experiment covered the time frame between December 2nd 2011 and March 2nd 2012, with a 7 days sampling rate. Gaps in the time series were caused by operational constraints related to the maintenance of the instrument, mostly due to bad weather conditions. The complete dataset is provided as supplementary material (Appendix A).

2.2. Preparation of sediment trap samples

The sediment trap samples were wet-sieved through 1 mm and 500 µm meshes before being splitted into four aliquots. A quarter of each sample was used for foraminiferal analysis, as was the material trapped into the meshes of 1 mm and 500 µm. After the wet-sieving process, the > 125 µm fraction was used for species identification and counting. This size fraction was chosen because it covers the size range of recent assemblages and also contains all foraminifera > 150 µm, which are usually used for paleoceanographic studies (Al-Sabouni et al., 2007; Zaric et al., 2005). The samples were analyzed wet allowing the quantification of fragile taxa, which could disintegrate during drying. Wet picking was performed using a transparent gridded tray for zooplankton analysis. Benthic foraminifera were not found in the samples. The chosen species *Globigerinoides ruber*, *Trilobatus sacculifer*, *Orbulina universa* and *Neogloboquadrina dutertrei* were the most abundant ones, together representing more than 70 % of the assemblage in most samples. The counts of the two varieties of *Globigerinoides ruber* (white and pink) were added for the flux calculation and later analysis. No further distinction of *T. sacculifer* or a distinction between *G. ruber* and *G. elongatus* was made.

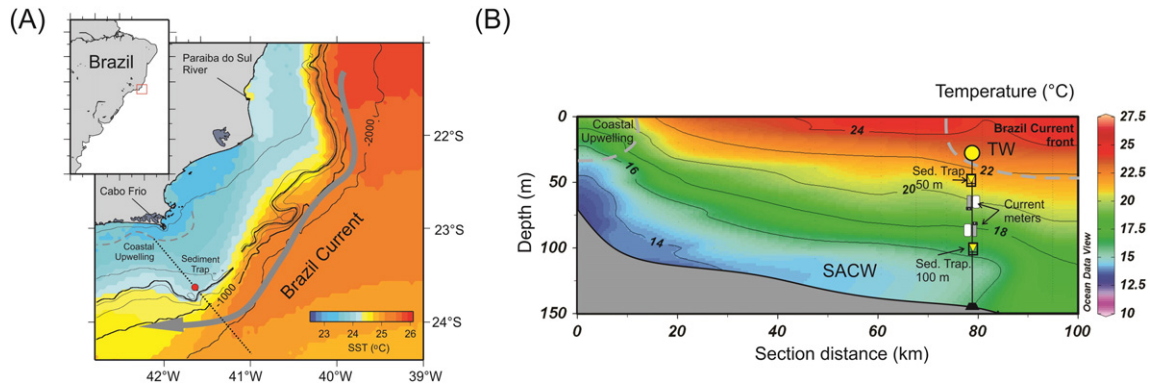


Fig. 1. (A) Study area and oceanographic features. The mooring site is marked with a red circle. (B) Cross-shelf section showing the thermal gradient with isotherms, the main water masses SACW (South Atlantic Central Water) and TW (Tropical Water), and the position of the sediment traps and the current meters. Temperature data was extracted from the World Ocean Data Center and cross-shelf plot was generated with Ocean Data View (Schlitzer, 2014).

2.3. Evaluation of vertical mobility and possible lunar periodicities in the foraminifera record

The focus of this work was to determine whether lunar-induced cycles could be detected in the time series of vertical fluxes of planktonic foraminifera species. Therefore, it is important to understand how the fluxes evolve in comparison to the succession of lunations (average time for the synodic month, or the mean interval between two successive new moons) throughout the sampling period. To this end, we employed three different approaches to compare the flux data to the lunar periodicities for a given species: (i) with the day numbering sequence throughout the sampling periods; (ii) with the evolution of the lunar cycle expressed as the sequence of lunar brightness; and (iii) with the sequential, discrete lunar phases.

2.3.1. Census and flux calculation of the planktonic foraminifera species

Foraminiferal fluxes were calculated based on the duration of sampling for each bottle of the sediment trap (sampling rate) and the area of the sediment trap (0.25 m²). The bulk sample was wet sieved over 1 mm and 500 µm meshes and all foraminifera were counted in these fractions. The residue was split using a rotary splitter into four aliquots and the foraminifera were counted in one aliquot and multiplied by four for the calculation of total abundances. The picked specimens were transferred to cardboard slides and identified under a stereomicroscope. Abundances and fluxes for the chosen species are provided as supplementary material (Appendix A). The fluxes were converted to a logarithmic scale for all further analysis, except for the raw flux plots in Figs. 2 and 6. The log-transformation was performed because subsequent statistical analyses require normal distribution of the data.

2.3.2. Flux dataset – day numbering sequence

The second step was to present the fluxes from the two traps as a function of time. Day counting comprises all the time intervals related to the four moorings. The onset and the end of the time series were defined at the first (#1) and last (#486) days of the months when the first and last deployments occurred. For each sample, its corresponding day # was attributed to the middle day # of each sampling interval (from first to fourth experiment: 3-, 7-, 5- and 7-day days sampling intervals, respectively; see Section 2.1). Days #12 and #477 correspond to the first and last collected samples. This approach allowed us to prepare flux data and day# datasets for each planktonic foraminiferal species, which were then employed for qualitative analysis of flux evolution throughout the sampling periods. The entire dataset is provided as supplementary material (Appendix A).

2.3.3. Flux dataset – lunar phase and brightness

Each day # of the overall sampling period was associated to its correspondent percentage value of moon brightness at midnight (information extracted from Astronomical Applications Department website of the U.S. Naval Observatory (<http://aa.usno.navy.mil/data/docs/MoonFraction.php>)). This strategy allowed us use the moon brightness datasets as a function of the day#. The percentage of lunar brightness can be associated with the moon phases as follows: New Moon (NM; 25–0 %); First Quarter (FQ; 25–75%); Full Moon (FM; 100–75 %); and Last Quarter (LQ; 75–25 %).

2.3.4. Variability of the vertical migration

In order to evaluate if lunar-induced periodicities could be related in some way to vertical migration during the reproductive cycle of each foraminiferal species, we calculated species-specific vertical flux proportionality between the traps at 50 m and 100 m depths using the following equation:

$$M_{sp,LPB} = \left\{ \frac{\left[\frac{\Phi_{100m}}{\Phi_{TOT}} \right]}{\left[\frac{\Phi_{50m}}{\Phi_{TOT}} \right]} \right\}_{sp,LPB}$$

where $M_{sp,LPB}$ is the vertical flux proportionality for a given species sp and brightness of lunar phase (LPB), while Φ_{100m} , Φ_{50m} and Φ_{TOT} are the absolute mean log-transformed fluxes of the 50m and 100m traps and the total flux, respectively. The total flux is the sum of the fluxes from both traps for a given species during a certain lunar phase. The equation employs the flux at the deeper trap as the numerator, since we expect a migration towards greater depths during gametogenesis (Erez et al., 1991). Values of $M_{sp,LPB}$ of 1.0 would imply that the flux of all dead shells originates from the water column shallower than 50 m. Higher values would indicate that a progressively larger part of the shelf flux derive from specimens that died below 50 m. Lower values could only occur in case of large lateral advection or in the case where the shallower trap collects live specimens.

2.4. Periodic regression

The possible link between fluxes and lunar cycles was tested by periodic regression analysis. In this analysis, the independent variable is an angular representation of time and this approach was demonstrated to be robust in order to detect lunar periodicity (deBruyn and Meeuwig, 2001). Furthermore, the analysis gives information about the timing of the maximum peak in the dataset and provides an equation, which can be used to estimate values for a given period. The methods and advantages in detecting lunar and seasonal cycles are summarized by deBruyn and Meeuwig (2001) and Jonkers and Kucera (2015), respectively. In this approach, we also used the log-transformed flux data

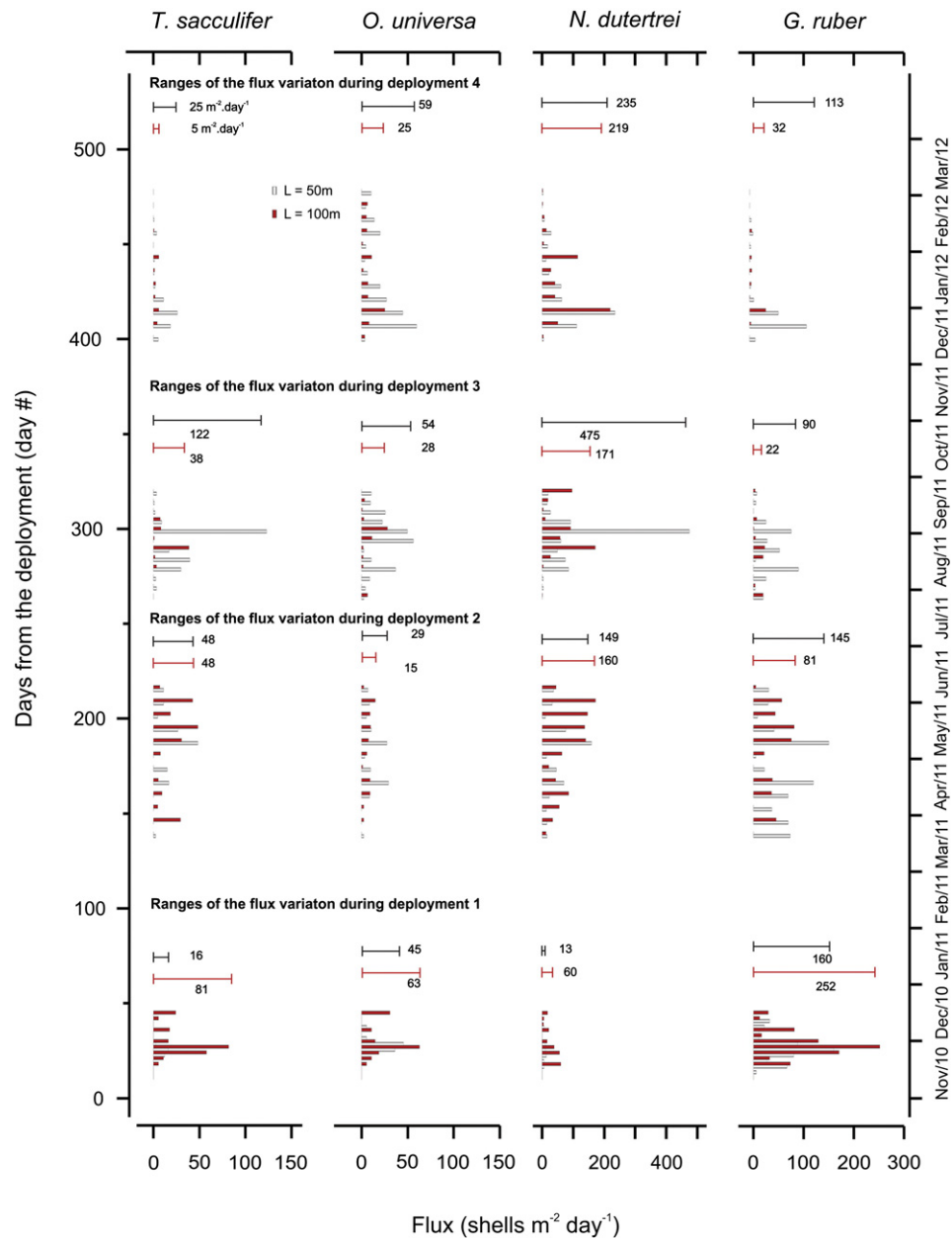


Fig. 2. Planktonic foraminifera shell fluxes from the southwestern Atlantic for the entire time series. The time series is exhibited in sequential days (left axis), as described in the methods, and monthly (right axis). The white bars represent the fluxes for the upper trap ($L = 50\text{m}$) and the red bars the fluxes for the deeper trap ($L = 100\text{m}$). Ranges of the fluxes in both traps are represented by black (50m) and red (100m) lines.

with the lunar days. The zero values were replaced by half of the minimum flux value for each deployment dataset. The observations time scale was converted to lunar days (LD) and posteriorly transformed in radian units ($\text{LD}/29 \times 2\pi$). In order to test the cycles the following model was applied to observations:

$$F(t) = A + B_{\sin(t)} + C_{\cos(t)}$$

where $F(t)$ is the shell flux at a given time and A-C are the parameters that will be estimated in the analysis.

The significance of the periodic regression analysis was evaluated using ANOVA for multiple regression and the results are summarized in Table 1. Due to the small number of data points in each time series, spectral analysis was not used in the dataset. An approach with spectral analysis cannot be expected to produce robust results with our time series data.

3. Oceanographic setting

The mesoscale surface circulation of the western boundary of the South Atlantic is dominated by the warm and nutrient-poor Brazil Current (BC) (Fig. 1), arising from the bifurcation of the South Equatorial Current (SSEC), typically located around 10°S , where two branches are generated with the North Brazil Current (NBC) flowing to the north and the Brazil Current (BC) flowing southward to the Brazil-Malvinas Convergence Zone (BMCZ) (Peterson and Stramma, 1991). As discussed by Walsh (1988), tropical areas of continental shelves that are linked to the western edge of oceanic systems are often related to less productive oceanic margins. However, mesoscale processes related to the dynamics of BC (encroachment, topographic acceleration, meandering and eddies) may induce the rise of cold and nutrient-rich South Atlantic Central Water (SACW) on the shelf, forming an upwelling system in the southeastern portion of the Brazilian shelf (Campos et al., 2000; Castelao and Barth, 2006; Silveira et al., 2008; Belem et al., 2013).

Table 1

Results from the periodic regression analysis and ANOVA for each species in both traps for the entire time series. The first panel (a) represents the upper trap and the panel below (b) represents the lower trap.

(a)

	Upper Trap/Deployment														
	1			2			3			4			all		
Species	peak	r ²	p-value	peak	r ²	p-value	peak	r ²	p-value	peak	r ²	p-value	peak	r ²	p-value
<i>G. ruber</i>	6.2	0.33	0.06	25.5	0.23	0.13	14.2	-0.10	0.63	3.8	-0.18	0.86	5.8	-0.02	0.55
<i>T. sacculifer</i>	5.7	0.56	0.01	27.5	0.01	0.38	24.7	-0.03	0.47	4.6	-0.18	0.86	2.3	0.01	0.29
<i>N. dutertrei</i>	4.6	0.50	0.02	24.5	0.17	0.18	26.0	-0.13	0.71	0.4	-0.21	0.97	2.2	-0.02	0.56
<i>O. universa</i>	9.4	0.49	0.02	25.2	0.15	0.19	22.9	0.01	0.38	4.2	-0.21	0.97	8.2	-0.04	0.83

(b)

	Lower Trap/Deployment														
	1			2			3			4			all		
Species	peak	r ²	p-value	peak	r ²	p-value	peak	r ²	p-value	peak	r ²	p-value	peak	r ²	p-value
<i>G. ruber</i>	5.9	0.50	0.01	23.3	-0.17	0.84	9.8	0.25	0.11	11.3	-0.15	0.75	7.8	0.02	0.26
<i>T. sacculifer</i>	4.1	0.28	0.08	18.0	-0.10	0.62	4.3	-0.19	0.90	12.8	-0.10	0.64	6.0	-0.02	0.65
<i>N. dutertrei</i>	5.1	-0.05	0.52	18.2	-0.06	0.52	7.7	-0.05	0.51	12.4	-0.14	0.72	8.5	0.01	0.28
<i>O. universa</i>	4.2	0.39	0.04	18.9	-0.13	0.71	8.8	-0.04	0.49	10.4	-0.06	0.52	6.8	0.05	0.11

The continental shelf off southeastern Brazil, especially between 21°S and 25°S, is widely studied because of this upwelling system (Ikeda et al., 1974; Matsuura, 1996; Castro and Miranda, 1998; Rodrigues and Lorenzetti, 2001; Castelao and Barth, 2006; Castelao, 2012; Cerda and Castro, 2014; Castro, 2014). The BC flows southward along the shelf break and slope of the Brazilian margin, as a component of the South Atlantic subtropical gyre, acquiring intensity and speed southward of the Abrolhos Bank (Silveira et al., 2000). As shown in Fig. 1, this boundary current carries the Tropical Water (TW) at the upper layers of the water column, as well as the South Atlantic Central Water (SACW) at an intermediate depth southwards (Stramma and England, 1999). Therefore, the shallower trap (50 m) is more influenced by the TW and the deeper trap (100 m) by the SACW. The material collected by the deeper trap (100 m) is derived from both layers, while the shallower trap (50 m) material is mostly derived from the surface layer (TW), although SACW intrusions can be observed on the temperature dataset for both traps. TW and SACW, besides the Coastal Water (CW) and the Subtropical Shelf Water (STSW), are the main water masses in the upper part of the water column of the southeastern Brazilian margin (Castro and Miranda, 1998; Castro, 2014; Venancio et al., 2014).

4. Results

4.1. Planktonic foraminifera fluxes

Among the foraminifera species analyzed in this study, *G. ruber* and *N. dutertrei* exhibited the highest flux variability throughout the sampling period (Fig. 2). *G. ruber* showed fluxes ranging from 0 - 160 shells m⁻² day⁻¹ and 0 - 252 shells m⁻² day⁻¹, whereas *N. dutertrei* fluxes ranged between 0 - 475 shells m⁻² day⁻¹ and 0 - 219 shells m⁻² day⁻¹ for the shallower and deeper trap, respectively. *Trilobatus sacculifer* exhibited a flux variation from 0 - 122 shells m⁻² day⁻¹ for the L = 50 m trap and 0 - 81 shells m⁻² day⁻¹ for the L = 100 m trap. The narrowest ranges were observed for *O. universa*, for which the fluxes varied between 0 - 59 shells m⁻² day⁻¹ in the shallower trap and between 0 - 63 shells m⁻² day⁻¹ in the deeper trap. In summary, *N. dutertrei* and *T. sacculifer* show a higher flux in the shallower than in the deeper trap (although for *N. dutertrei* this pattern may be caused by a single data point during the third deployment), whereas *G. ruber* was the only species that exhibited higher flux in the deeper trap. Fluxes at L = 50 m and L = 100 m appeared to be rather similar for *O. universa*.

Furthermore, we noted several striking patterns for the fluxes from the first to fourth deployments, especially from the *G. ruber*, *T. sacculifer* and *N. dutertrei*, which can be summarized by three observations: (i) the highest fluxes occurred at the first deployment (day # 12 - # 45; November - December 2010) for *G. ruber* and *O. universa*, and at the third deployment (day # 264 - # 319; July - September 2011). For *N. dutertrei* and *G. sacculifer*; (ii) an opposite trend can be observed for the fluxes of *G. ruber* (decreasing) in comparison to the *N. dutertrei* (increasing) from the first to the fourth deployment; and, interestingly (iii) for all species, the observed range variation for flux values at L = 100m were higher than in its counterpart at L = 50m at the first deployment whereas an opposite pattern was observed for third (day # 264 - # 319; July - September 2011) and fourth (day # 400 - # 477; December 2011 - February 2012) deployments.

4.2. Periodic regression

The results from the periodic regression demonstrate that there is a relationship between the lunar cycle and the foraminiferal fluxes for the first deployment (Table 1). However, the pattern does not hold when the entire time series is analyzed (Table 1). Data from the analysis is plotted only for the first deployment, which has the higher sampling resolution (3 days) and covers a full cycle, and for the entire time series (Fig. 3). The data for the first deployment systematically show highest fluxes for the first 3-7 lunar days and lowest around the 18-20 lunar days. For all species in both traps, except *O. universa* (L = 50m), the peaks are situated between 4 and 6 days after the full moon. The periodic regression against lunar day of the time series for the first deployment (Table 1) shows in most of the analyzed time series (per trap and species) that the periodic model with a synodic months period is statistically significant (*p*-value < 0.05) and explains about 50% of the variance in the data. The correlation values are surprisingly high, considering that our model assumes that the lunar reproductive cycle is the only factor modulating the shell flux of planktonic foraminifera. In contrast, periodic regression of shell flux series for the other three deployments and for the entire time series showed no clear pattern. This may indicate that the lunar signal is not constantly present with the same peak timing, or that its expression in the shell flux series may be masked by another environmental factor. An approach using spectral analysis would be able to disentangle even such a complex cyclic pattern in the lunar frequency band, but unfortunately such analyses is hampered by the presence of sampling gaps between the deployments.

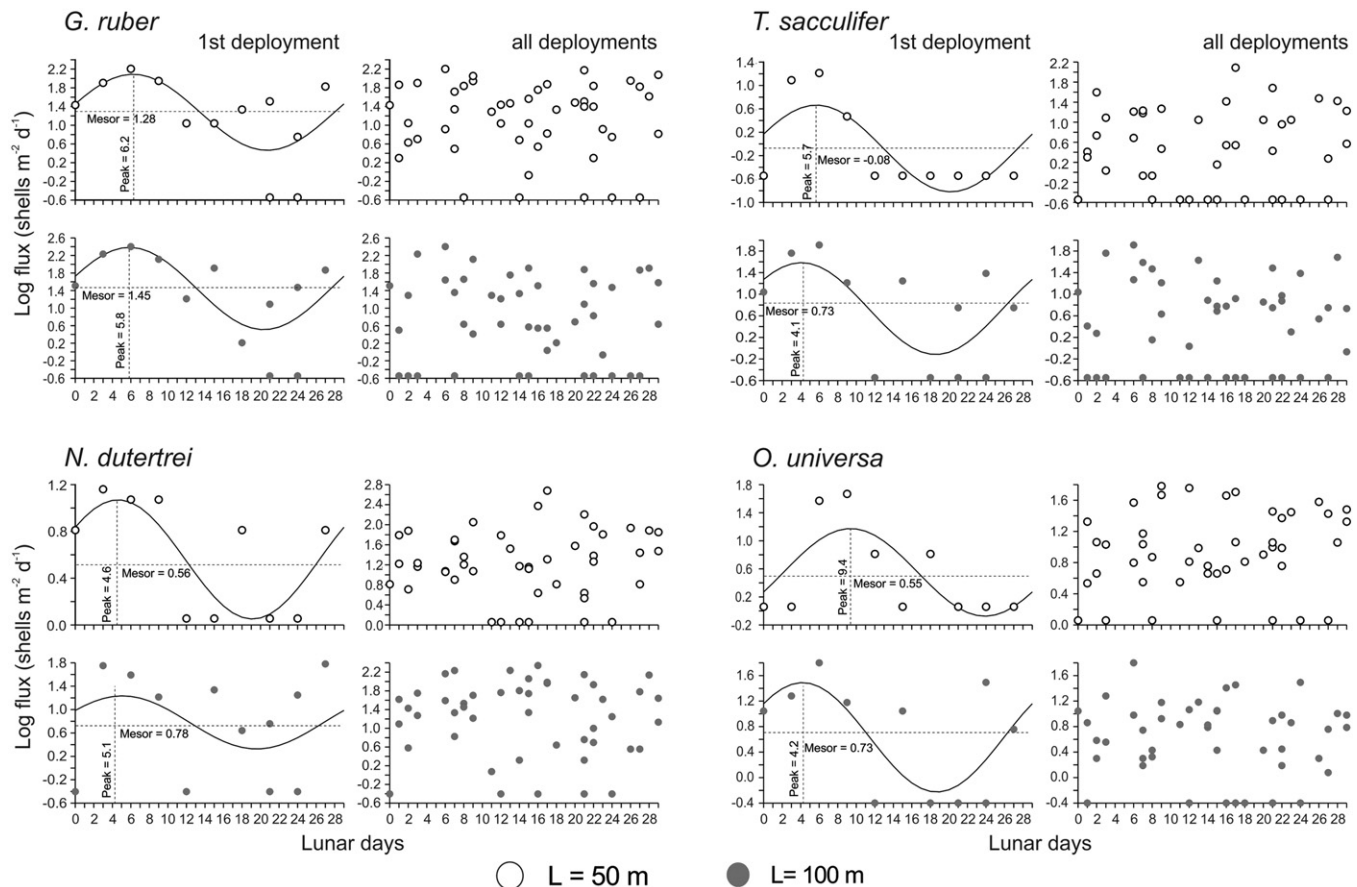


Fig. 3. Log-transformed fluxes plotted against the lunar days. The periodic regression and its parameters are plotted for each species for the first deployment. The thick black line represents the best fit. The horizontal dashed line is the periodic mean (mesor) and the vertical dashed line is peak time. The entire time series is exhibited without the parameters. Data from the upper trap ($L = 50$ m) is represented by white circles and from the deeper trap ($L = 100$ m) by grey circles.

4.3. Lunar phase vs. foraminifera flux datasets

In order to investigate whether flux variability corresponds to moon brightness and phases, we calculated mean fluxes for each moon phase (specifically, at its corresponding brightness interval). This approach allowed us to compare, for each trap, the mean log flux for each brightness interval and the corresponding moon phase – throughout the entire lunation (Fig. 4).

Considering all deployments, from the NM to the first half of FQ, all species except *T. sacculifer* exhibited higher mean log fluxes at the $L = 50$ m trap compared to the $L = 100$ m trap. The mean log fluxes for *G. ruber*, *N. dutertrei*, *O. universa* and *T. sacculifer* show no significant change for the shallow trap during this period. From the first to the second half of the FQ, mean log fluxes for *G. ruber* at $L = 50$ m decreased, while for $L = 100$ m an increasing trend can be inferred for all species. An increase in the mean log flux values for both traps can be observed for all species except *O. universa* throughout the FM phase (first to second half). After the FM phase, distinctive flux patterns were observed for each species. For *G. ruber* and *N. dutertrei*, a decrease of mean log flux values for the shallow trap can be observed from the second half of the FM to the first half of LQ. Particularly, the $L = 100$ m mean log flux for *T. sacculifer* remained relative constant while at $L = 50$ m such values decreased from second half of FM to the first half of LQ.

For all species, the mean log fluxes increase at both traps from the first to the second half of LQ. It is also noticeable that during the second half of the LQ, the four species exhibited maximal mean log fluxes for at least one trap, suggesting that the second half of the FQ may be related to the period of higher foraminifera shell deposition. For the upcoming NM, we observed a decrease in mean log fluxes for all species and both

traps. This pattern suggests a connection between the lunar phase or moon brightness and mean foraminiferal fluxes patterns for the four chosen species throughout lunations, as will be discussed later.

4.4. Vertical migration

Vertical migration of the foraminifera species between both traps (Fig. 5) was assessed for all deployments by the vertical flux proportionality, as outlined in Section 2.3. Despite the assumption that the flux proportionality is directly linked to the vertical migration process, other potential biases, such as lateral advection, may influence the signal. These potential biases will be addressed in the discussion. Vertical migration is commonly associated with spinose species, since they are believed to shed their spines and sink to deeper waters to initiate gametogenesis. This process may be triggered by changes in light intensity as they sink below the photic zone (Erez et al., 1991).

We observe values lower than 1.0 for the vertical migration during almost all lunar phases for *G. ruber* and *O. universa*, except on the first half of the LQ for *O. universa*. These values could indicate that lateral advection or collection of live non-sinking specimens in the shallower trap influence their fluxes. However, for *T. sacculifer*, especially during the LQ and NM, we observe values higher than 1.0, which indicate that a large part of the flux during these phases is composed by specimens that died below 50 m. Values higher than 1.0 are also observed for *N. dutertrei*, although the variation is weaker. Despite these observations, all the species have their minimum ratio values during the NM phase that occur right after the LQ and at the first half of the FQ, and their maximum ratio values during the LQ, which indicate that all species have higher flux values in the deeper trap (100 m) during the last quarter.

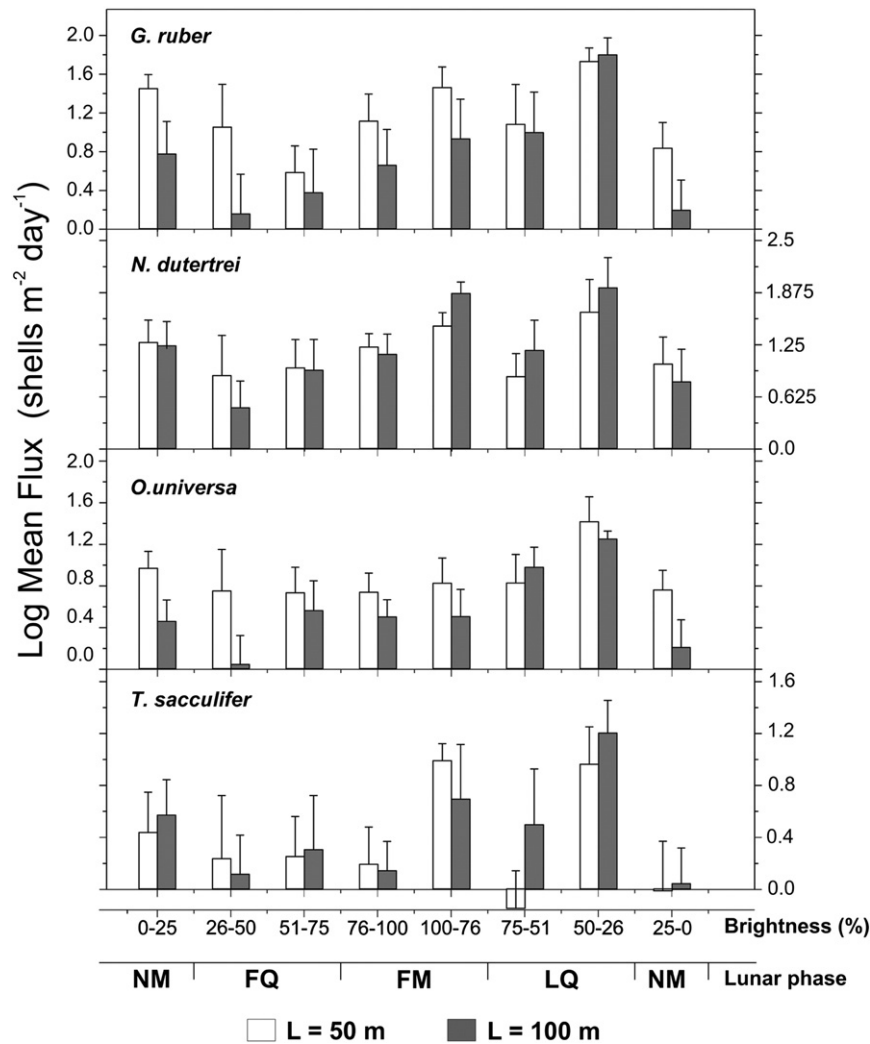


Fig. 4. Mean log-transformed fluxes per lunar phase using all deployments. The intervals for each phase were defined using the lunar brightness values. The white bars represent the data from the upper trap (L = 50 m) and the grey bars from the deeper trap (L = 100 m). The bars represent the mean logarithmic flux for each phase and the lines above each bar represent the standard deviation.

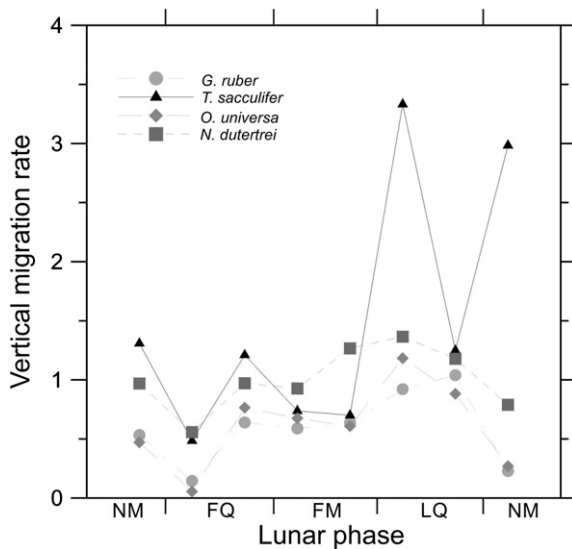


Fig. 5. Estimate of the vertical migration for each species per lunar phase. The vertical flux proportionality is described in the methods (Section 2.3) and represents the difference of fluxes between the traps.

5. Discussion

5.1. Lunar reproduction cycles

Previously, lunar cyclicity in planktonic foraminiferal reproduction was studied from sediment traps moored at 100 m or deeper (Kawahata et al., 2002; Lončarić et al., 2005; Lin, 2014; Jonkers et al., 2015). In our study, the sediment traps were placed in a shallow water column on the continental shelf and not deep in the open ocean. Hence, lateral advection could potentially transport planktonic foraminifera and bias the flux rates recorded in the traps. The current-meter data (Appendix B) shows indeed mean current velocities higher than 12 cm/s (Baker et al., 1988) and an influence of lateral advection on our planktonic foraminiferal fluxes seems possible. However, this putative influence is difficult to quantify, since we did not perform measurements of size or density of the foraminiferal shells. These parameters are crucial for the determination of particle velocities and consequently the potential alteration of fluxes caused by lateral transport (Baker et al., 1988). Assuming a large size fraction (>125 μm) and a density value higher than 1.6 g/cm³, which would be reasonable since calcite density is close to 2.71 g/cm³, the flux change could vary from -50% to +40%, which means that the trap efficiency could either decrease or increase (Baker et al., 1988). Furthermore, other studies pointed out that the traps may catch larger foraminifera with higher

efficiency, since the hydrodynamics for solid particles is different from that for fine particles or aggregates (Gardner, 2000; Yu et al., 2001). Consequently, we can neither exclude nor quantify a potential bias through lateral advection. However, as pointed out by Zaric et al. (2005), even if the lateral component in particle fluxes cannot be excluded, lateral displacement is likely not a significant factor affecting sediment trap time series, when the size and weight of foraminiferal shells are considered. We also note that in our case, the vertical profile of current velocity and current direction appears to have remained relatively stable between deployments (Appendix B) and should have thus affected all sampling periods equally.

The shallow water depth of our trap location might also lead to generally lower abundance of planktonic foraminifers, compared to the open ocean locations, due to ecological exclusion (Schmuker, 2000). However, if lunar cycles exist, they should still be present in our time series, because foraminifera occur abundantly on the studied outer shelf. The mean fluxes observed in the studied period (Fig. 2) correspond well to those reported for the same subtropical province (Bé, 1977) by Lončarić et al. (2005), indicating that the flux recorded by the trap corresponded to a normal population that was not significantly affected by ecological exclusion from the shallow shelf.

Because of the shallow position of our sediment traps, it cannot be excluded that a certain part of the flux represents living specimens that were caught by the traps during passive or active vertical migration in the upper water layer. We consider the shallow position of the trap unlikely to have biased the results because the mixed layer in the region is typically shallower than 50 m (Cerdeja and Castro, 2014) and the flux of trapped specimens should have been proportionate to the population density (Fig. 3). Irrespective of the presence or absence of a lunar reproductive cycle, the trapping of live specimens would thus only elevate the baseline flux value, but not induce any artificial cycles.

Due to the shallow position of the traps, resuspension of sediments from the sea floor could be another potential bias. However, our analysis of the current meter data (Appendix C) demonstrated that resuspension is restricted to 5 meters above the seafloor and very probably did not reach the traps. The study of Albuquerque et al. (2014) also pointed out that resuspension was either not significant or even non-detectable in these experiments.

Assuming that the flux variability represents a largely undisturbed vertical flux of a representative population of planktonic foraminifera, we can search for the signature of lunar synchronization. The periodic regression for the first (3 day resolution) deployment shows that in both traps and for all species, except *O. universa* ($L = 50\text{m}$), there is a significant periodic component with a peak approximately 4 to 6 days after the full moon (Fig. 3). However, the periodic regression for the other deployments, and the entire time series showed no regular peak time. Our results for the first deployment could be in agreement with reproduction triggered by the full moon, but we stress that the period of reproductive cycle may be not stable. In the case of reproduction triggered by the full moon, the reproductive process would begin at or shortly after the full moon, be completed within about a day (compare reproductive cycle duration for *H. pelagica*, Spindler et al., 1979) with dead shells arriving in the trap almost immediately afterwards. Such a synchronization would also be consistent with the large drop in shell fluxes in the period immediately following the high-flux interval. This drop in shell flux may represent a period where most of the population consists of small juveniles not captured by the trap and where the adult population responsible for the observed shell flux has been largely depleted by the reproductive event. This interpretation requires that not all specimens of the analyzed species participated in the synchronized reproduction, but a smaller part of the adult population remained alive and contributed to the shell flux outside the main reproductive window (Bijma et al., 1990a). Depending on species and trap depth, the shell flux associated with the reproductive window after the full moon would account for 31–52 % of the total flux of that species when

all deployments are considered together, except for 21 % of *T. sacculifer* flux for the shallow trap (Fig. 4).

The relationship between the putative reproductive event and the lunations as observed in our data is consistent with that deduced for *H. pelagica* by Spindler et al. (1979) and for *G. ruber* in the Gulf of Mexico by Jonkers et al. (2015). The observation of *T. sacculifer* decreasing in abundance in plankton tows already during the full moon (Bijma et al., 1990a) may also be consistent with reproduction after the full moon. If we assume that, the pattern observed by Bijma et al. (1990a) represents a vertical migration (see also Erez et al., 1991) prior to reproduction, as also indicated by the higher flux of this species in the deeper trap observed in our data (Fig. 5). However, since the mean current speeds are higher than 10 cm/s in our region, the interpretation of the vertical flux proportionality may be biased.

Jonkers et al. (2015) showed that *O. universa* and *T. sacculifer* shell fluxes in the Gulf of Mexico peaked at the full moon and Kawahata et al. (2002) also observed peaks in flux at full moon for *T. sacculifer*. Because in both cases the traps were deployed deeper ($> 400\text{m}$) than in our study (50 and 100m) these observations can only be interpreted as a primary offset comparative to our results, with reproduction being triggered prior to full moon. These findings indicate that the flux peaks may not consistently correspond to a specific lunar phase. It is possible that the exact phasing depends on location or reflects the influence of other environmental factors that modulate the factor triggering reproduction. Another possibility is that intensified sedimentation of planktonic foraminifera species due to the formation of aggregates (Turner, 2002) is affecting the flux pattern, which would also lead to synchronous fluxes. However, foraminiferal tests are quite large compared to other particles and do not need to be scavenged in order to sink (De La Rocha and Passow, 2007). In fact, De La Rocha and Passow (2007) observed a very low correlation ($r^2 = 0.25$) between POC and foraminiferal fluxes at an Atlantic site. In addition, aggregates only seem to have major influence on the transport of juvenile planktonic foraminifera (Bé et al., 1985), which were not analyzed here. Based on the previous arguments, we think that aggregate formation plays a minor role in the flux variations and is not very a likely cause of synchronous flux patterns. We note that both in our study and in that by Jonkers et al. (2015) almost all analyzed species had synchronous peak fluxes. This may indicate that the reproduction is triggered collectively, but the exact period (lunar phase) when all species present peak fluxes may vary.

The temporal stability of the flux peaks in the studied species has been investigated by joint analysis of flux data covering the entire deployment period of one year. Whereas the periodic regression fails to identify any cyclicity in the merged data (Fig. 3), the mean fluxes for each lunar phase (Fig. 4) indicate a common pattern of higher fluxes at the end of the last quarter. Instability of the period between two reproductive events would lead to precisely such a weakening of the periodic signal. This effect is further enhanced by the coarser resolution of the remaining part of the flux series, such that the periodic signal is no longer detectable. Similar phenomena can provide an explanation for the results by Lončarić et al. (2005), who found pronounced lunar cyclicity in the spectral analysis only for *H. pelagica*. We speculate that the strict endogenous timing of reproduction of *H. pelagica* (Spindler et al., 1979) leads to a strong signal in the flux data despite the low resolution (8 days) of the traps. In contrast, the synchronization of reproduction in the remaining species may follow an external trigger, leading to variable period and signal attenuation in the flux data.

Our results thus seem to support the hypothesis that reproductive synchronization occurs in planktonic foraminifera. This reproductive mode seems to be widespread among planktonic foraminifera (Jonkers et al., 2015), but it is still not clear whether it is present universally, whether it occurs in all marine provinces and whether and how it is related to lunar cyclicity. Similar to the findings of Jonkers et al. (2015) we detected a lunar cycle in the flux series of *N. dutertrei* (Fig. 3). Interestingly, this species shows higher fluxes in the deeper

trap for most of the trap series, suggesting that a significant portion of the population constantly lives below 50 m, which is consistent with a deeper habitat indicated for this species by geochemical studies (e.g., Wejnert et al., 2013). Clearly, the short-term dynamics of planktonic foraminiferal populations, including their reproductive behavior, still deserves further investigations, and studies applying stratified high-resolution sediment trap designs have an excellent potential to support such investigations. Although lunar reproductive cycles appear to play an important role for the modulation of the foraminiferal fluxes, there is not yet a consensus regarding the timing of the flux, the involved species, and if the cycle is endogenous or triggered by an exogenous force.

5.2. Other factors controlling the fluxes of planktonic foraminifera

In order to understand the short-term (lunar) variability in planktonic foraminifera shell fluxes, other environmental factors influencing their magnitude and also the detectability of the lunar periodicity have to be taken into account. Sediment trap studies have shown that planktonic foraminiferal fluxes can be influenced by seasonality, physical circulation patterns, productivity and the species reproductive cycles

(Sautter and Thunell, 1991; Kincaid et al., 2000; King and Howard, 2001; Kawahata et al., 2002; Zaric et al., 2005; Rigual-Hernández et al., 2012).

Among these factors, sea-surface temperature is one of the most important parameters controlling the distribution and abundance of planktonic foraminifera (Bé and Tolderlund, 1971). Thermal preferences are different between planktonic foraminiferal species, which could explain interspecific flux differences (Bijma et al., 1990b; Zaric et al., 2005). Food supply can be also an important factor modulating foraminiferal fluxes (Watkins et al., 1996). Species without symbionts, like *G. bulloides*, are dependent on the productivity of the environment, while species with symbionts benefit from the photosynthetic activity and are more independent in respect to changes in food supply (Sautter and Thunell, 1991; Watkins et al., 1996). For symbiont-bearing species like *G. ruber* the light intensity and consequently the depth of the photic zone is also a relevant element. Other possible influences are vertical advection, i.e. up- or downwelling and the intensity of lateral displacement.

To place the probable influence of lunar cyclicity on the foraminiferal fluxes into a longer-term context, we plotted the flux of *G. ruber* for the shallower and deeper traps throughout the entire time series period

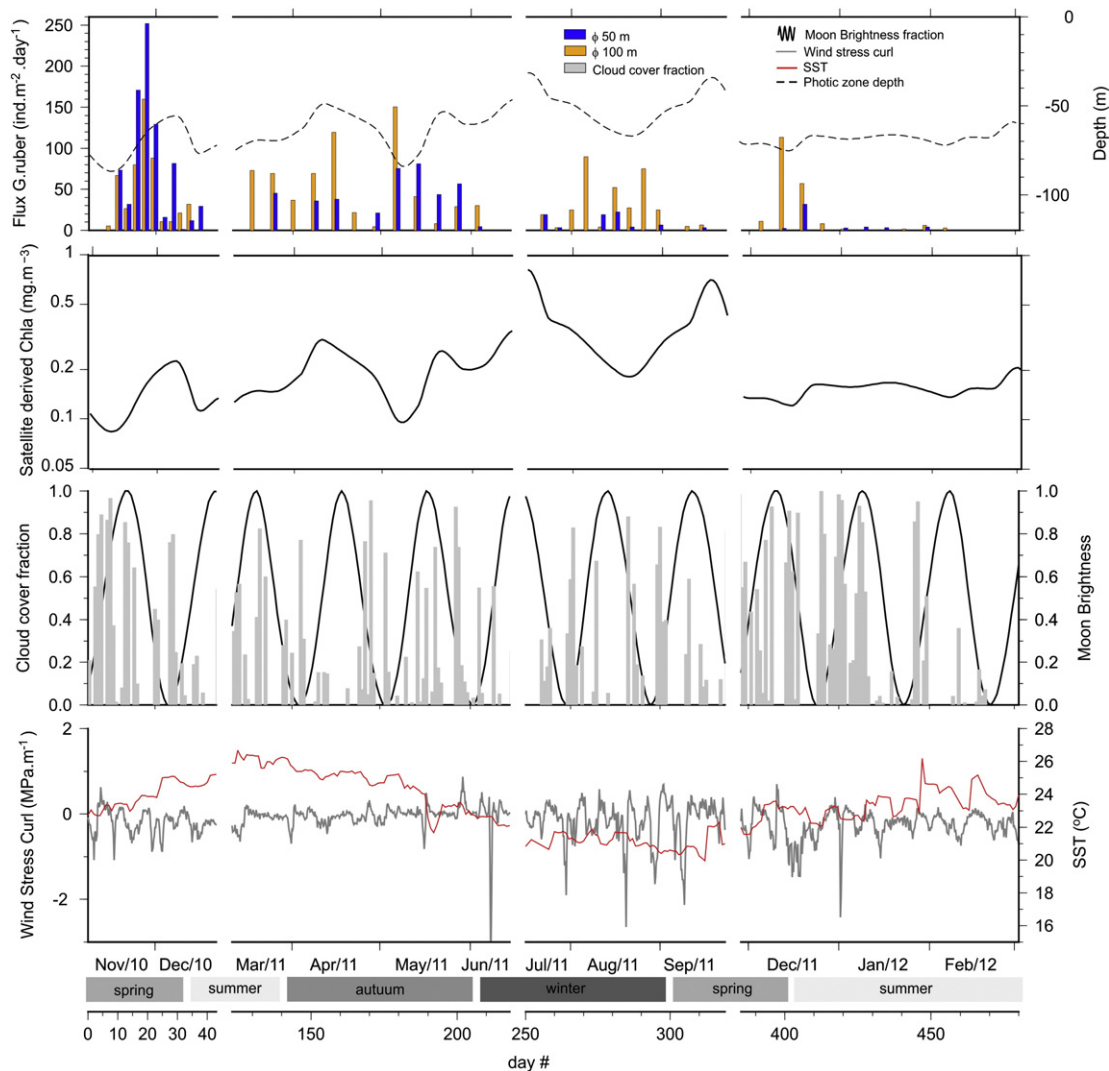


Fig. 6. Fluxes of *G. ruber* for the entire time series exhibited with multiple parameters. Colored bars represent the *G. ruber* fluxes for 50 m (blue) and 100 m (yellow). The dashed line represents the depth of the photic zone estimated from MODIS/AQUA Chlorophyll 8-day data. The solid black line in the panel below represents the Chlorophyll-a derived from MODIS/AQUA. The moon brightness (thick black line) is plotted with the cloud cover (grey bars) indicating periods with high/low light intensity. Cloud cover was extracted from the NASA catalog dataset (OMTO3e). The SST (red line) is plotted with the wind stress curl (grey line) showing the main physical oceanographic parameters that influence the study area. Temperature was extracted from NOAA OceanWatch program (ID: satellite.BA.ssta.5day) and wind stress curl data is derived from NOAA CoastWatch (ID: erdQAdivmodmday).

along other parameters (temperature, depth of the euphotic zone, chlorophyll and wind stress curl) in order to assess other factors controlling the flux (Fig. 6). The variability of productivity, inferred from the chlorophyll concentration and consequently the depth of the euphotic zone can cause changes in the foraminiferal fluxes (Watkins et al., 1996). However, in our data, the variability of the chlorophyll concentration or the depth of the euphotic zone does not show any direct relationship to the fluxes. There does not seem to be any phase lag relationship either, linking episodes of higher food availability earlier to higher flux later (Fig. 6).

Alternatively, for symbiont-hosting species, the intensity of light might be an important factor influencing their symbiont activity. To test whether times with higher light intensity are indeed associated with higher fluxes, we compared the fluxes with moon brightness and cloud coverage (Fig. 6). Although we do not observe any direct effect of cloud coverage on flux timing or magnitude, there may be a relationship between cloud coverage and moon phase on the triggering of reproduction. For example, during the high-resolution sampling period in November 2010, the sky was cloudy during full moon and maximum fluxes appeared 5–7 days after the full moon. A similar situation occurred in December, April and August 2011, whereas peak flux occurred at full moon, when the sky was cloudless. These observations would support an exogenous forcing of the lunar cycles in species other than *H. pelagica*, as suggested by Jonkers et al. (2015).

A closer investigation of *G. ruber* fluxes in other deployments of our time series is further hampered by the significant decrease of *G. ruber* fluxes from spring 2011 to winter 2012 (Fig. 6). This steady decrease in the fluxes of *G. ruber* is probably linked to seasonal variability (Sautter and Thunell, 1991; Jonkers and Kucera, 2015). A decrease in *G. ruber* fluxes occurs in periods with lower temperature and higher variability of the wind stress curl. This wind stress curl variability is related to the intrusions of the SACW in the upper layers at our site (Castelao and Barth, 2006). Since *G. ruber* is a species related to warm and oligotrophic waters, these conditions are unfavorable for the population (Bé and Tolderlund, 1971). At the same time, these conditions are favorable for *N. dutertrei* (Fig. 2), which is associated with lower temperatures, variations in the thermocline depth and increased productivity (Sautter and Thunell, 1991). Thus, we can conclude that the seasonal variability is an important modulator of planktonic foraminiferal fluxes on longer than monthly time scales in this area. Jonkers et al. (2015) in the Gulf of Mexico also noticed the influence of seasonal trend in the shell fluxes and its influence on the detection of lunar cycles.

6. Conclusions

We found evidence for synchronized fluxes of four species of planktonic foraminifera (*G. ruber*, *T. sacculifer*, *N. dutertrei* and *O. universa*) at the continental margin off Brazil in the southwestern Atlantic Ocean. For the first deployment, the shell fluxes increase after the full moon, with the highest flux rates during the last quarter. Periodic regression indicates that the maximum flux occurs approximately 4–6 days after full moon. These findings appear consistent with the concept of reproduction in planktonic foraminifera being episodic and synchronized by lunar periodicity. However, periodic regression for the other deployments and for the entire dataset suggests that the period of the reproductive cycle cannot be strictly synchronous with the phases of the moon during each month. Although the reproductive cycle is not the only factor that determines the flux of planktonic foraminifera in the water column, this study demonstrates its relevance in modulating fluxes of *G. ruber*, *T. sacculifer*, *N. dutertrei* and *O. universa*. These are clearly episodic with peaks accounting for up to one half of total flux. Whilst the average spacing of the peaks seems to point to lunar periodicity, the reproduction in these species is unlikely to be controlled by an endogenous clock. Instead, we suggest that lunar reproductive cycles may be triggered by an exogenous factor and the variable expression of this factor between months leads to uneven peak spacing. Further

high-resolution studies are needed to better constrain the lunar modulation of foraminiferal carbonate export to the sea floor.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.marmicro.2016.03.003>.

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