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



Igor M. Venancio ^{a,b,*}, Daniel Franco ^c, Andre L. Belem ^d, Stefan Mulitza ^a, Michael Siccha ^a, Ana Luiza S. Albuquerque ^b, Michael Schulz ^a, Michal Kucera ^a

^a MARUM—Center for Marine Environmental Sciences and Faculty of Geosciences, University of Bremen, D-28359 Bremen, Germany

^b Departamento de Geoquímica, Universidade Federal Fluminense, Outeiro de São João Batista, s/n°., Niterói, Rio de Janeiro, CEP: 24020-141, Brazil

^c Coordenação de Geofísica, Observatório Nacional, R. Gal. José Cristino, 77, 20921-400 Rio de Janeiro, RJ, Brazil

^d Departamento de Engenharia Agrícola e Meio Ambiente, Universidade Federal Fluminense, Niterói, Rio de Janeiro 24210-240, Brazil

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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. © 2016 Elsevier B.V. All rights reserved.

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

E-mail address: ivenancio@marum.de (I.M. Venancio).

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

^{*} Corresponding author at: MARUM—Center for Marine Environmental Sciences and Faculty of Geosciences, University of Bremen, D-28359 Bremen, Germany.

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 (Khripounoff 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 biweekly 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 $> 125 \,\mu m$ 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 foraminifers 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.

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