

**First-order estimate  
of the planktic  
foraminifer biomass**

R. Schiebel and  
A. Movellan

# First-order estimate of the planktic foraminifer biomass in the modern global oceans

**R. Schiebel and A. Movellan**

LUNAM Université, Université d'Angers, Laboratoire des Bio-Indicateurs Actuels et Fossiles (BIAF), CNRS, UMR6112, LPGN, 2 Boulevard Lavoisier, 49045 Angers CEDEX 01, France

Received: 20 March 2012 – Accepted: 10 April 2012 – Published: 27 April 2012

Correspondence to: R. Schiebel (ralf.schiebel@univ-angers.fr)

Published by Copernicus Publications.

This discussion paper is/has been under review for the journal Earth System Science Data (ESSD). Please refer to the corresponding final paper in ESSD if available.

Title Page

Abstract

Instruments

Data Provenance & Structure

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

## Abstract

Planktic foraminifera are heterotrophic mesozooplankton of global marine abundance. The position of planktic foraminifers in the marine food web is different compared to other protozoans and ranges above the base of heterotrophic consumers. Being secondary producers with an omnivorous diet, which ranges from algae to small metazoans, planktic foraminifers are not limited to a single food source, and are assumed to occur at a balanced abundance displaying the overall marine biological productivity at a regional scale. We have calculated the assemblage carbon biomass from data on standing stocks between the sea surface and 2500 m water depth, based on 754 protein-biomass data of 21 planktic foraminifer species and morphotypes, produced with a newly developed method to analyze the protein biomass of single planktic foraminifer specimens. Samples include symbiont bearing and symbiont barren species, characteristic of surface and deep-water habitats. Conversion factors between individual protein-biomass and assemblage-biomass are calculated for test sizes between 72 and 845  $\mu\text{m}$  (minimum diameter). The calculated assemblage biomass data presented here include 1057 sites and water depth intervals. Although the regional coverage of database is limited to the North Atlantic, Arabian Sea, Red Sea, and Caribbean, our data include a wide range of oligotrophic to eutrophic waters covering six orders of magnitude of assemblage biomass. A first order estimate of the global planktic foraminifer biomass from average standing stocks ( $>125 \mu\text{m}$ ) ranges at 8.5–32.7 Tg C yr<sup>-1</sup> (i.e. 0.008–0.033 Gt C yr<sup>-1</sup>), and might be more than three times as high including the entire fauna including neanic and juvenile individuals adding up to 25–100 Tg C yr<sup>-1</sup>. However, this is a first estimate of regional planktic-foraminifer assemblage-biomass (PFAB) extrapolated to the global scale, and future estimates based on larger data-sets might considerably deviate from the one presented here. This paper is supported by, and a contribution to the Marine Ecosystem Data project (MAREDAT). Data are available from [www.pangaea.de](http://www.pangaea.de) (<http://doi.pangaea.de/10.1594/PANGAEA.777386>).

## First-order estimate of the planktic foraminifer biomass

R. Schiebel and  
A. Movellan

Title Page

Abstract

Instruments

Data Provenance & Structure

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## 1 Introduction

Planktic foraminifers are marine protozoans with calcareous shells and chambered tests. Most of the ~50 modern (morpho-) species live in surface waters down to the deep chlorophyll maximum of the oceans, and in marginal seas like the Caribbean and Red Sea (Bijma and Hemleben, 1994; Schmuker and Schiebel, 2002). Planktic foraminifers are largely absent from shallow marginal seas like the North Sea (Hemleben et al., 1989). Most of the modern morpho-species are ubiquitous. Highest diversity is recorded from temperate to subtropical waters. Due to meso-scale and local hydrographic features the distribution of planktic foraminifers is patchy on various temporal and spatial scales (e.g. Siccha et al., 2012). Margins of subtropical gyres and hydrographic fronts are characterized by allochthonous species expatriated by currents (Weyl, 1978).

Planktic foraminifers are affected by the availability of food, and the range of temperature and salinity, as well as chemistry of the ambient seawater (e.g. Bé, 1977; Hemleben et al., 1989; Bijma et al., 1990; Ortiz et al., 1995; Schiebel et al., 2001; Lombard et al., 2011). Species abundance varies with season, water mass, and water depth (e.g. Schiebel et al., 2001). The vertical separation of species is more evident in the tropics than in polar regions, owing to a wider diversity of hydrographic and biotic variables from surface to depth at low latitudes compared to the more uniform water column at high latitudes (Schiebel and Hemleben, 2005, and references therein). The seasonal distribution pattern of planktic foraminifers is most pronounced in high and mid latitudes, following phytoplankton succession and availability of food. In polar oceans, a single maximum of planktic foraminiferal production occurs during summer, when euphotic conditions allow for enhanced primary production (Spindler and Dieckmann, 1986; Volkman, 2000). In mid latitudes, two seasons of enhanced production occur during spring and fall (Schiebel and Hemleben, 2005). At low latitudes, seasonality is low, and productivity follows regional conditions like monsoonal activity and upwelling intensity (Hemleben et al., 1989).

### First-order estimate of the planktic foraminifer biomass

R. Schiebel and  
A. Movellan

Title Page

Abstract

Instruments

Data Provenance & Structure

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



**First-order estimate  
of the planktic  
foraminifer biomass**R. Schiebel and  
A. Movellan[Title Page](#)[Abstract](#)[Instruments](#)[Data Provenance & Structure](#)[Tables](#)[Figures](#)[⏪](#)[⏩](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

At a global scale, the abundance of planktic foraminifers follows the overall pattern of primary productivity (Schiebel, 2002). In turn, non-lagged correlations of primary productivity and planktic foraminifer abundance are weak at a regional scale (Schiebel, 2002), possibly because of the omnivorous diet of planktic foraminifers in the marine food web, and phase shifts in the production of phytoplankton and zooplankton (Hemleben et al., 1989). Non-spinose species are largely herbivorous, and spinose species accept a wide variety of animal prey, including larger metazoans such as copepods, pteropods, and ostracods (Anderson et al., 1979; Caron and Bé, 1984; Spindler et al., 1984). Intermediate-dwelling species are believed to feed on settling organic matter (Itou et al., 2001). Predators specialized on planktic foraminifers have not yet been identified.

Shallow-dwelling species are shown to reproduce once or twice (one species only) per month. Intermediate to deep-dwelling species reproduce less often (Hemleben et al., 1989). Not all specimens reach the reproductive ontogenetic stage during one reproductive cycle and may reproduce later. Growth and abundance of juveniles depends on ecological conditions. Fast growth and high survival rates occur if the diet is abundant. The prolocular ontogenetic stage consists of a first chamber built of calcite and ranges at 12–25  $\mu\text{m}$  in diameter (Brummer and Kroon, 1988). The first juvenile chambers are formed on a sub-daily rate, and during ontogeny the speed of chamber formation gradually decreases. The neanic stage is marked by a change in depth habitat, and occasional changes in selection of diet (Brummer and Kroon, 1988). Adult specimens consist of 10–20 chambers, and tests are between 100 and 1000  $\mu\text{m}$  in size (on average  $\sim 250 \mu\text{m}$ ).

The intra-shell cytoplasm of planktic foraminifers is differentiated from reticulate and rhizopodial cytoplasm outside of the test (Hemleben et al., 1989). Cytoplasm reaches far into the ambient seawater along spines, and occasionally forms a rhizopodial net. Food in form of lipids and starch is stored in special vacuoles (Schiebel and Hemleben, 2005). Symbiont-bearing species depend on light and are restricted to the euphotic layer, and subsurface to deep-dwelling species are symbiont-barren (e.g. Bé, 1982).

## First-order estimate of the planktic foraminifer biomass

R. Schiebel and  
A. Movellan

Title Page

Abstract

Instruments

Data Provenance & Structure

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Although planktic foraminifers are major producers of marine calcareous shells (called tests), they constitute only a minor portion of total zooplankton. Consequently, planktic foraminifers have been major target of research in geology and paleoceanography since the 1960s (e.g. Bé, 1977; Vincent and Berger, 1981; Hemleben et al., 1989; and references therein). Planktic foraminifer biomass was first analysed for three species and 112 individuals from surface water pump samples off Bermuda in 1991 and 1992 (Michaels et al., 1995). The species analysed by Michaels et al. (1995) are present also in our data set, and discussed in comparison to our protein biomass data. Conversion factors between carbon-biomass and volume range between 0.018 and 0.18  $\text{pg C } \mu\text{m}^{-3}$  with an average of  $0.089 \pm 0.055 \text{ pg C } \mu\text{m}^{-3}$ , and an average C:N of 5.8 (Michaels et al., 1995).

The objective of this paper is the construction of a database on live planktic foraminifer abundance and biomass, which includes a wide range of water depths, and modern productivity regimes between the tropical and polar oceans, and finally an estimate of the planktic foraminifer biomass. The conversion from abundance to assemblage biomass is based on a first data set on the species and size specific protein biomass. Extrapolating from the resulting regional and seasonal biomass data, a first-order global estimate of the modern planktic foraminifer biomass is given.

## 2 Material and methods

Planktic-foraminifer assemblage-biomass (PFAB) was calculated for 6100 size fractions from 1057 plankton net samples from the North Atlantic Ocean, Caribbean, Arabian Sea and Gulf of Aden, and Red Sea (Table 1), comprising faunal data from the equatorial to polar oceans (Fig. 1), obtained between 1989 and 1999 (Fig. 2). A large part of the samples were obtained within the German contribution to the Joint Global Ocean Flux Studies in the 1990s, at stations and transects in the North Atlantic (BIO-TRANS) and Arabian Sea repeatedly sampled at seasonal and regional resolution, over a wide range of global marine primary productivity from oligotrophic to eutrophic

conditions. Planktic foraminifer protein biomass was obtained from 754 individuals, including 21 species and morphotypes from all ontogenetic stages (Table 2). The average planktic-foraminifer assemblage-biomass was calculated for average test-size frequencies in seven test-size bins (Table 3), and standing stocks at water-depths intervals between the surface ocean and 2500 m depth (Table 4). Construction of the data-set is explained in Fig. 3.

## 2.1 Sampling and faunal counts

A multinet with five 100- $\mu\text{m}$  nets and a rectangular opening of 0.25 m<sup>2</sup> (HYDROBIOS midi) was applied for vertical hauls at 0.3–0.5 ms<sup>-1</sup> towing speed (cf. Schiebel et al., 1995). Standardized water depth intervals of between 80–100 m allowed direct comparison of data from different sampling campaigns (Schiebel, 2002). Samples were preserved in a 4 % formalin-seawater solution and buffered with hexamine at a pH of 8.2. Classification and faunal counts were carried out on test size fractions >100-125-150-200-250-315  $\mu\text{m}$  and >315  $\mu\text{m}$  with an incident binocular microscope using the taxonomy of Hemleben et al. (1989). Live individuals were differentiated from empty tests according to the presence or absence of cytoplasm, respectively. Daily to inter-annual data sets were combined, and regional data sets from different oceans were calibrated for their taxonomy and processing method. To avoid bias in the faunal data resulting from possible under-sampling close to the mesh-size (100  $\mu\text{m}$ ) of the plankton net, the faunal data analysed here ( $n = 6100$ ) refer to the size fraction >125  $\mu\text{m}$ . Census data are available from the Pangaea database at the AWI (Bremerhaven, Germany, www.pangaea.de).

## First-order estimate of the planktic foraminifer biomass

R. Schiebel and  
A. Movellan

Title Page

Abstract

Instruments

Data Provenance & Structure

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## 2.2 Protein measurement

### 2.2.1 Sampling of live planktic foraminifers for protein measurement

Live planktic foraminifers were sampled on three research-cruises in the subtropical to temperate eastern North Atlantic and temperate western North Pacific (Table 2). From R/V *Poseidon* cruise 349 in waters off the Azores Islands from 5 to 24 April 2007, 133 live specimens of planktic foraminifers from seven stations and were sampled from discrete water depth intervals, classified, and deep-frozen individually before analyses in the laboratory. From the R/V *Meteor* cruise 84/5, 31 May to 21 June 2011, in the Bay of Biscay, 413 live planktic foraminifers were analyzed. From the R/V *Tansei-Maru* cruise KT11-20, 21–25 August 2011, in the Pacific off northeastern Honshu, Japan, 213 live foraminifers were analyzed. Specimens sampled during the latter two cruises were analysed for their protein content on board the research vessel immediately after sampling. Analyses of the test morphometry and weight were carried out at the University of Angers.

A total of 754 foraminifers were analyzed from 18 sites and water depths ranging from 0 to 1500 m (Table 2). Planktic foraminifers were sampled with a 100- $\mu$ m plankton-net. Specimens were classified and processed individually. Live individuals were selected for their presence of cytoplasm. Each foraminifer was transferred into a bath of micro-filtered seawater, gently cleaned with a brush to remove all particles stuck to the specimen including organic matter. Subsequently, specimens were immersed in de-ionised water for less than a second to remove the seawater. Each foraminifer was individually stored in an Eppendorf cup, and frozen at  $-80^{\circ}\text{C}$  (R/V *Poseidon* 349), or immediately analysed for protein content (R/V *Meteor* 84/5 and *Tansei-Maru* KT11-20).

### 2.2.2 Planktic foraminifer protein analyses using nano-spectrophotometry

Protein biomass of planktic foraminifers was analysed with the Bicinchoninic Acid Method (BAM) developed by Smith (1985), using a mix of copper solution (4 % (w/v)

ESSDD

5, 243–280, 2012

## First-order estimate of the planktic foraminifer biomass

R. Schiebel and  
A. Movellan

Title Page

Abstract

Instruments

Data Provenance & Structure

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



**First-order estimate  
of the planktic  
foraminifer biomass**R. Schiebel and  
A. Movellan

Title Page

Abstract

Instruments

Data Provenance &amp; Structure

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

CuSO<sub>4</sub> · 5H<sub>2</sub>O solution; Sigma-Aldrich) and bicinchoninic acid (BCA; Sigma) solution (Smith et al., 1985; Zubkov and Sleight, 1995; Mojtahid et al., 2011). In contact with proteins the Cu<sup>2+</sup> ions of the copper solution are reduced to Cu<sup>+</sup>. The Cu<sup>+</sup> ions react with the BCA, and a strong purple color is produced. The intensity of the color increases proportionally with the protein concentration, and the absorbance of the 562 nm wave length was measured with a nano-spectrophotometer on 2 µl of sample or standard solution (NanoDrop 2000, Thermo Scientific). Protein standard solution consists of Bovine Serum Albumine (BSA) of known concentration. Each sample and standard solution was measured in triplicate (Movellan et al., 2012). Foraminifer samples and protein standard solutions were prepared at the same time to make sure that the incubation time and temperature were identical.

Immediately after the foraminifers were cleaned and stored in Eppendorf cups, or after being unfrozen in case of the R/V *Poseidon* 349 samples, 20 µl of micro-filtered tap water was added to each Eppendorf cup for 30 min to allow for an osmotic shock to quantitatively expose the foraminifer cytoplasm, and 400 µl of working reagent (WR) was added (Movellan et al., 2012).

The reaction and resulting coloration of the sample solution depends on incubation time and temperature, which was adjusted to the foraminifer protein contents. An optimum color spectrum was obtained at an incubation time of 24 h at room temperature (20 ± 2 °C). After incubation, each tube was centrifuged for 3 s at 5000 rpm, and the absorbance at 562 nm was measured with a NanoDrop 2000 nano-spectrophotometer. The absorbance of the WR is affected both by color and brightness resulting from the concentration of proteins. Each absorbance value was measured three times, and standard curves were constructed using polynomial regression.

The efficiency and yield of the osmotic shock method for cytoplasm exposure was tested on 24 specimens of *Globorotalia hirsuta*, *Globorotalia scitula*, and *Globigerinella siphonifera* from R/V *Poseidon* 349 samples. The three species were chosen for their different test architectures and apertures, i.e. globular with wide apertures (*G. siphonifera*), discoidal with intermediate-sized apertures (*G. hirsuta*), and discoidal with



small apertures (*G. scitula*). Cytoplasm and proteins were exposed to the WR by crushing the foraminifer tests. The protein data of the crushed specimens were compared to specimens of the same species and size, which were subjected to an osmotic shock for cytoplasm exposure.

### 5 2.3 Morphometric analyses and weight of the foraminifer test

After protein analyses, the foraminifer tests were carefully cleaned with tap water to remove particles and stains of the WR. The tests were then stored individually in microslides. Each test was photographed from the apertural side with an automated incident light microscope installed at the University of Angers, and driven by analySIS<sup>®</sup> software (Bollmann et al., 2005; Clayton et al., 2009), at a resolution of 1.4  $\mu\text{m}^2$  (pixel size), and images were analysed for their two-dimensional (silhouette) morphometry. Minimum diameter and silhouette area were used for analyses of the protein-to-size relation of the planktic foraminifer tests (Figs. 4 and 5).

A microbalance (Mettler Toledo XP2U, readability of 0.1  $\mu\text{g}$ ) was employed to weigh individual foraminifer tests. Weighing was carried out in an air-conditioned weighing-room at constant temperature and humidity. Each foraminifer was individually stored in an aluminium capsule and weighed after >12 h of acclimatisation in the weighing room. All foraminifer tests were weighed three times, at an overall average precision of  $\pm 0.17 \mu\text{g}$ .

### 20 2.4 Quality control

All of the data points on planktic-foraminifer assemblage-biomass presented here are calculated from own data on population dynamics (faunal data, standing stocks), and individual protein biomass data. All of the data points on standing stocks protein biomass were individually verified. In case any data point deviated from data points of similar context, i.e. protein biomass data from similar species and size, and faunal data from similar locations and water depths, those data were rejected. All zero values

## First-order estimate of the planktic foraminifer biomass

R. Schiebel and  
A. Movellan

Title Page

Abstract

Instruments

Data Provenance & Structure

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



(i.e. empty tests) were removed from the individual protein biomass data, as well as protein biomass values, which were unreasonable considering the size and test-weight of a species. In turn, zero values were kept in the data set on standing stocks, since the water column (in particular at greater depth) can be devoid of live planktic foraminifers.

5 We did not apply Chauvenet's criterion to remove outliers from our data set, because (i) we could verify all of the data presented here, which were all produced at our laboratory and assumed reliable, and (ii) the maximum values are included in the natural variability of standing stocks and assemblage biomass.

### 3 Results

#### 10 3.1 Efficiency of the BAM for planktic foraminifer protein biomass determination

The protein data derived from specimens treated with an osmotic shock (standard method) were compared to data from 24 crushed specimens of *G. hirsuta*, *G. scitula*, and *G. siphonifera* from the same samples (R/V *Poseidon* 349) using variance analysis (performed with the software R v.12.2.1). The protein contents of crushed specimens (15 of *G. hirsuta* and *G. siphonifera* are not significantly different from the specimens submitted to an osmotic shock ( $p = 0.5929$  and  $0.3312$ , respectively). We hence conclude that the standard BCA method (i.e. osmotic shock) provides reliable protein data for these two species representative of all species of the data set including 704 individuals (i.e. 94.7 % of the data set on protein biomass; Table 2). In contrast, the protein content (20 of *G. scitula* was significantly larger for crushed specimens (average  $2.416 \mu\text{g}$ ) than for the specimens subjected to an osmotic shock (average  $2.238 \mu\text{g}$ ;  $p = 0.02465$ ), i.e. the method resulted in a yield 92.59 %. The slight underestimation of the measured protein content of *G. scitula* using the osmotic shock method may results from the compact test (25 architecture and the small aperture of this small globorotalid species. The same might be true for the globorotalid species *G. truncatulinoides*. Since both species *G. scitula*

## First-order estimate of the planktic foraminifer biomass

R. Schiebel and  
A. Movellan

Title Page

Abstract

Instruments

Data Provenance & Structure

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



and *G. truncatulinoidea* include only 5.3% of the biomass data set, and <1% of the faunal data, we did not correct the following assemblage biomass calculations for this bias.

### 3.2 Planktic foraminifer biomass, test size and weight

Individual planktic foraminifer biomass is related to test size (Fig. 4). The average protein biomass of the two smallest planktic foraminifer test size bins >100–125  $\mu\text{m}$  and >125–150  $\mu\text{m}$  is similar at 0.7  $\mu\text{g}$  per specimen (Table 3), and significantly ( $t_{99\%}$ ) increases in the larger size bins (Table 3, Fig. 5). The small size bins contribute more to the PFAB (Table 3) because of a much higher frequency of small than large specimens to the overall standing stocks (Peeters et al., 1999; Schiebel and Hemleben, 2000). The protein-biomass of different species, and the planktic-foraminifer assemblage-biomass (PFAB) from different latitudes (Fig. 6) and different months and seasons (Fig. 7) are similar. The average global individual planktic foraminifer protein-biomass is calculated at 0.845  $\mu\text{g}$  (Table 3).

PFAB as a function of water depth is highest in the upper 60 m of the water column, and decreases by two orders of magnitude to a water depth of 1000 m (Table 4, Fig. 8). The highest variation in individual biomass occurs at intermediate water depths from 100–700 m (Fig. 8). In turn, species and size-specific individual biomass is not related to water depth, as shown for *Globorotalia hirsuta* (Fig. 9). The average global depth-integrated biomass of planktic foraminifers per meter square down to 2500 m water depth is 11.27 mg (Table 4).

The  $\text{CaCO}_3$  mass (i.e. weight) of planktic foraminifer tests analysed here was on average three times as high as the protein biomass (Fig. 4a and b). Given a theoretical  $\text{CaCO}_3$  mass of planktic foraminifer tests of  $100.09 \text{ g mol}^{-1}$ , and a carbon mass of  $12.01 \text{ g mol}^{-1}$ , the planktic foraminifer test calcite-carbon mass resembles ~36% of the protein biomass.

## First-order estimate of the planktic foraminifer biomass

R. Schiebel and  
A. Movellan

Title Page

Abstract

Instruments

Data Provenance & Structure

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



### 3.3 Seasonal development of the planktic foraminifer assemblage biomass (PFAB)

Seasonal changes in PFAB are most pronounced in surface waters. The highest PFAB in the temperate North Atlantic at BIOTRANS (around 47° N, 20° W) occurred in spring (March and April), and affected waters down to 300 m water depth (Fig. 10). Intermediate PFAB occurred in surface waters during summer, and lowest PFAB occurred in surface and deep waters occurred in fall and later winter (Fig. 10).

Highest PFAB in the Arabian Sea occurred in July and August, i.e. during the fully developed SW monsoon (Fig. 11), with concentrations similar to those during spring in the North Atlantic (Fig. 10). In contrast to the North Atlantic, very high PFAB in the Arabian Sea was more restricted to the surface 100 m of the water column (Fig. 11). Lowest PFAB in the Arabian Sea occurred in late March to April, i.e. during the spring intermonsoon. During the late NE monsoon (early to mid March), PFAB in the Arabian Sea was slightly higher than during the intermonsoon (Fig. 11).

### 3.4 Regional differences in PFAB

Lowest average PFAB occurred in the subtropical North Atlantic, in the central and equatorial Arabian Sea, and in the Red Sea (Fig. 12). Average PFAB in subtropical gyre south of the Azores Islands in the eastern North Atlantic was one order of magnitude lower than the PFAB at mid latitudes (Fig. 12). The further north in the eastern North Atlantic the more limited is the PFAB to the short productive season. The maximum PFAB concentration of  $>200 \mu\text{g m}^{-3}$  at 68° N in July was quantitatively similar to that in spring at 47° N (Fig. 12). Highest PFAB concentration of  $>100 \mu\text{g m}^{-3}$  in the Arabian Sea around 17° N, 60° E occurred in surface waters at the upwelling region off Oman, and affected also the subsurface ( $>100$  m depth) water column (Figs. 11 and 12). In general, average PFAB exponentially decreases with water depth between 100–1500 m (Fig. 8) in regions and during times of low biological productivity, and is

enhanced down to water depth >1000 m in regions and at times of high productivity (Figs. 10 to 12).

#### 4 Biomass conversion factors

The protein-biomass of planktic foraminifers measured by nano-spectrophotometry, and the resulting biomass conversion factors calculated from our data are similar to those given by Michaels et al. (1995) from CHN analyses. An average species of 315- $\mu\text{m}$  minimum test diameter contains about 2.2  $\mu\text{g}$  protein biomass (Fig. 4a), which amounts to 2.2  $\mu\text{g}$  per  $10^5 \mu\text{m}^2$  silhouette area (Fig. 4b), the latter being a reliable measure of the foraminifer test volume (Beer et al., 2010). The resulting biomass conversion factor of  $0.092 \pm 0.070 \text{ pg C } \mu\text{m}^{-3}$  is similar to the average value of  $0.089 \pm 0.055 \text{ pg C } \mu\text{m}^{-3}$  given by Michaels et al. (1995) without specifying the size of the analysed specimens. However, Michaels et al. (1995) analysed the same species *O. universa* and *H. pelagica*, which are also frequent in our data on larger subtropical species (Table 2). Based on this inter-comparison, we conclude that the protein biomass equals the amount of cytoplasm carbon (see also Zubkov et al., 1999). In contrast, smaller specimens have much higher average conversion factors of  $0.413 \pm 0.040 \text{ pg C } \mu\text{m}^{-3}$  (at 100  $\mu\text{m}$  minimum test diameter) than larger specimens (deduced from Fig. 4a and b). Consequently, we have based our biomass calculations on average biomass conversion factors for different test-size bins (Table 3), resembling those also applied to the analyses of the live planktic foraminifer population dynamics (e.g. Schiebel and Hemleben, 2000). We assume that the individual planktic foraminifer cytoplasm (including the reticulate and rhizopodial cytoplasm) was quantitatively sampled, and we do not account for any symbiont-biomass. Individual planktic foraminifer biomass appears to be independent of water depth (Fig. 9), though, and the same biomass conversion factors per size bin are applied to all analysed water depth intervals (Table 4).

## 4.1 First-order estimates of the global planktic foraminifer biomass

The majority of planktic foraminifers is living in the surface oceans, hemipelagic oceans, and marginal ocean basin (e.g. Vincent and Berger, 1981; Schiebel et al., 1995; Peeters and Brummer, 2002; Kuroyanagi and Kawahata, 2004; Loncaric et al., 2006; Retailleau et al., 2011), i.e. above and within the seasonal pycnocline (=thermocline) and associated deep chlorophyll maximum (DCM). Accordingly, largest regional and temporal variation in population dynamics occurs in surface waters (Schiebel, 2002). Diversity and turnover rates of the subsurface and deep dwelling fauna are much smaller than those of the surface dwelling fauna (Schiebel and Hemleben, 2005). Consequently, our calculation of the surface water PFAB is based on a data set of higher resolution than that of the subsurface to deep PFAB (Tables 1 and 2, Fig. 8).

Our data on the planktic foraminifer population dynamics in the eastern North Atlantic, Caribbean, Red Sea, and Arabian Sea (Table 1) cover a wide range of productivity regimes (Berger et al., 1988; Berger, 1989; Yoder et al., 1993; Antoine et al., 1996; Longhurst, 2007; the MODIS web site) from equatorial to subpolar latitudes, including oligotrophic waters of the subtropical gyres and upwelling regions (Fig. 12), and facilitate a first-order estimate of the global planktic foraminifer biomass. However, being omnivorous zooplankton the production of planktic foraminifers is not directly related to primary production (Schiebel, 2002). We have hence calculated the PFAB from regional data sets on population dynamics (numbers per  $\text{m}^3$ ) available from <http://doi.pangaea.de/10.1594/PANGAEA.777386>.

Considering the good data coverage between the tropical and polar oceans (Figs. 1 and 6), oligotrophic to eutrophic waters (Fig. 12; cf. Schiebel, 2002), and over the productive seasons (Fig. 7; cf. Obata et al., 1996, for seasonal changes in the surface ocean productivity) between the 1989 and 1999 (Fig. 2), the average PFAB  $>125 \mu\text{m}$  test size sums up to a global average of  $2.93\text{--}11.27 \text{ mg C m}^{-2}$  (geometric mean and arithmetic mean, respectively) at any point of time (Table 4:

ESSDD

5, 243–280, 2012

### First-order estimate of the planktic foraminifer biomass

R. Schiebel and  
A. Movellan

Title Page

Abstract

Instruments

Data Provenance & Structure

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

2934.11–11265.13  $\mu\text{g C m}^{-2}$ ). Planktic foraminifer biomass at waters deeper than 2500 m is assumed negligible here (cf. Schiebel, 2002).

To extrapolate from regional to global planktic foraminifer biomass, the absolute surface area of the global deep oceans is taken as  $290 \times 10^6 \text{ km}^2$  (Milliman and Droxler, 1996; total area =  $362.03 \times 10^6 \text{ km}^2$ , cf. Dietrich et al., 1975). This excludes areas of the global oceans, in which planktic foraminifer reproduction, and hence normal foraminifer production, is supposed to be inhibited due to, for example, shallow water depths, turbidity of the ambient seawater, or ice cover (Hemleben et al., 1989). The resulting global planktic foraminifer biomass would hence add up to 0.85–3.27 Tg C at any point of time. Assuming a global deep ocean surface of  $290 \times 10^6 \text{ km}^2$  inhabited by fully developed planktic foraminifer faunas might be a rather conservative guess, though, since Retailleau et al. (2009 and 2011) presented fully developed faunas in the marginal Bay of Biscay, like in all other marginal basins included in our estimate. Including marginal basins increases the ocean area inhabited by planktic foraminifers by  $32 \times 10^6$  to  $322 \times 10^6 \text{ km}^2$  (Milliman and Droxler, 1996), resulting in a global planktic foraminifer biomass of 0.94–3.63 Tg C at any point of time.

The average turnover time, i.e. the synodic lunar reproduction cycle of surface dwelling planktic foraminifer species is assumed to be one month (e.g. Schiebel and Hemleben, 2005, and references therein). The abundant shallow dwelling species *Globigerinoides ruber* (fortnightly reproduction) and possibly all deep dwelling globorotalids (up to annual reproduction cycles) are exceptions. Excluding aphotic (winter) conditions in mid to high latitudes, and assuming nine complete reproduction cycles on average, the global planktic foraminifer biomass ( $>125 \mu\text{m}$ ) amounts to  $8.5\text{--}32.7 \text{ Tg C yr}^{-1}$  (geometric mean and arithmetic mean, respectively; Table 4). Interannual variations in regional planktic foraminifer production (Schiebel and Hemleben, 2000) are assumed compensated at the global scale.

The above calculations include only the planktic foraminifer fauna  $>125 \mu\text{m}$ , though, excluding smaller individuals of  $\sim 12\text{--}125 \mu\text{m}$  in size (cf. Brummer and Kroon, 1988). Given that the number of individuals of a population decreases over time, and assuming

## First-order estimate of the planktic foraminifer biomass

R. Schiebel and  
A. Movellan

[Title Page](#)[Abstract](#)[Instruments](#)[Data Provenance & Structure](#)[Tables](#)[Figures](#)[⏪](#)[⏩](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

that the average faunal contribution of individuals  $>100\text{--}125\ \mu\text{m}$  in size amounts to 50% of the total fauna  $>100\ \mu\text{m}$  (Table 3; Schiebel and Hemleben, 2000), the above numbers ( $>125\ \mu\text{m}$ ) would possibly be twice as high when including individuals  $>100\text{--}125\ \mu\text{m}$ , and more than three times as high for the entire planktic foraminifer fauna including juvenile and neanic individuals. A conservative first-order estimate of the entire global planktic foraminifer biomass production might hence range at  $\sim 25\text{--}100\ \text{Tg C yr}^{-1}$ , which is about half that of the estimated diazotroph biomass (Luo et al., 2012: 40–200 Tg C), and  $\sim 3\text{--}5\%$  the biomass of diatoms (Leblanc et al., 2012:  $\sim 500\text{--}3000\ \text{Tg C}$ ).

## 4.2 Uncertainties of the PFAB estimates

This paper presents a first estimate of regional planktic foraminifer assemblage biomass (PFAB) extrapolated to the global scale, and future estimates based on larger data-sets might considerably deviate from the one presented here. We will therefore regularly update our data after having improved the spatial coverage of our data set, and overcome methodical problems. Although including wide geographical and ecological ranges, our data set lacks data from the Southern Hemisphere, and in particular data from the southern ocean would considerably improve our data set. In addition, we will try to include data on biomass and standing stocks of small (including juvenile and neanic) specimens, as well as data on the biomass of the symbionts of the symbiont-bearing planktic foraminifer species. So far, conversion of protein biomass to cytoplasm carbon has only been verified by comparison with literature data (Michaels et al., 1995) and would need to be confirmed by species- and size-specific data from different seasons and regions. Considering all of the uncertainties, the numbers given above need to be used with care, but seem to be quite reasonable in comparison to the data of other groups of plankton, i.e. diazotrophs and diatoms presented by Luo et al. (2012) and Leblanc et al. (2012).

## First-order estimate of the planktic foraminifer biomass

R. Schiebel and  
A. Movellan

Title Page

Abstract

Instruments

Data Provenance & Structure

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## 5 Conclusions

The protein biomass analysed with the Bicinchoninic Acid Method (BAM) using nano-spectrophotometry is assumed a reliable measure of the individual planktic foraminifer cytoplasm carbon content. From 754 cytoplasm carbon data of 21 planktic foraminifer species and morphotypes we have constructed a data set on the assemblage biomass carbon of the fauna >125 µm test size for a total of 1057 samples including 13 water-depth intervals between the ocean surface and 2500 m water depth. Samples from the North Atlantic, Caribbean, Red Sea, and Arabian Sea cover oligotrophic to eutrophic sites from equatorial to subpolar latitudes from different years and seasons. Assuming an ocean area of  $322 \times 10^6 \text{ km}^2$ , which supports planktic foraminifer production over nine month per year results in a global planktic foraminifer biomass of  $\sim 8.5\text{--}32.7 \text{ Tg C yr}^{-1}$ . Including juvenile and neanic planktic foraminifer <125 µm in size the total planktic foraminifer biomass is assumed at  $\sim 25\text{--}100 \text{ Tg C yr}^{-1}$ .

*Acknowledgements.* We thank crew and shipboard scientific parties for their help in sampling. We are particularly grateful to the chief scientists Sascha Flögel (R/V *Meteor* 84/5) and Takashi Toyofuku (R/V *Tansei-Maru* KT11-20) for their support in sampling. Chris Beer helped with sampling and sample processing on R/V *Poseidon* cruise 349. We are particularly grateful to Fabien Lombard and Meike Vogt who inspired the paper as a contribution to the ESSDD special issue on plankton biomass. Meike and other contributors to the ESSDD issue did a great job in organizing a large group of contributors, communicating the methodology, and practical support. We thank Stéphane Pesant for integrating our data in the Pangaea data archive, Erik Buitenhuis for the gridding of our data, Collen O'Brien for creating the standard set of MAREDAT plots, and Frans Jorissen for his helpful comments on an earlier version of our manuscript. The work of AM was financially supported by the Regional Council of the Pays de La Loire, France.

## First-order estimate of the planktic foraminifer biomass

R. Schiebel and  
A. Movellan

Title Page

Abstract

Instruments

Data Provenance & Structure

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

## References

- Anderson, O. R., Spindler, M., Bé, A. W. H., and Hemleben, C.: Trophic activity of planktonic foraminifera, *J. Mar. Biol. Assoc. UK*, 59, 791–799, 1979.
- Antoine, D., André, J.-M., and Morel, A.: Oceanic primary production, 2, Estimation at global scale from satellite (coastal zone color scanner) chlorophyll, *Global Biogeochem. Cy.*, 10, 57–69, 1996.
- Bé, A. H. W.: An ecological, zoogeographic and taxonomic review of Recent planktonic Foraminifera, in: *Oceanic Micropaleontology*, edited by: Ramsay, A. T. S., London, Academic Press, 1, 1–100, 1977.
- Bé, A. W. H.: Biology of Planktonic Foraminifera, *Foraminifera: Notes for a Short Course*, in: *Studies In Geology*, edited by: Broadhead, T. W., Univ. Tennessee, 6, 51–92, 1982.
- Beer, C. J., Schiebel, R., and Wilson, P. A.: Technical Note: On methodologies for determining the size-normalised weight of planktic foraminifera, *Biogeosciences*, 7, 2193–2198, doi:10.5194/bg-7-2193-2010, 2010.
- Berger, W. H.: Global Maps of Ocean Productivity, in *Productivity of the Ocean: Present and Past*, in: *Dahlem Workshop Reports*, edited by: Berger, W. H., Smetacek, V. S., and Wefer, G., *Life Sci. R.*, John Wiley, New York, 44, 429–455, 1989.
- Berger, W. H., Fischer, K., Lai, C., and Wu, G.: Ocean carbon flux: Global maps of primary production and export production, in: *Biogeochemical Cycling and Fluxes Between the Deep Euphotic Zone and Other Oceanic Realms*, edited by: Agegian, C., *NOAA Natl. Undersea Res. Prog. Res. Rep.*, 88, 131–176, 1988.
- Bijma, J. and Hemleben, Ch.: Population dynamics of the planktic foraminifer *Globigerinoides sacculifer* (Brady) from the central Red Sea, *Deep-Sea Res. Pt. I*, 41, 485–510, 1994.
- Bijma, J., Faber, W. W., and Hemleben, C.: Temperature and salinity limits for growth and survival of some planktonic foraminifers in laboratory cultures, *J. Foramin. Res.*, 20, 95–116, 1990.
- Bollmann, J., Quinn, P. S., Vela, M., Brabec, B., Brechner, S., Cortés, M. Y., Hilbrecht, H., Schmidt, D. N., Schiebel, R., and Thierstein, H. R.: Automated particle analysis: Calcareous microfossils, in: *Image Analysis, Sediments and Paleoenvironments*, edited by: Francus, P., Kluwer Academic Publishers, Dordrecht, The Netherlands, 229–252, 2004.
- Brummer, G. J. A. and Kroon, D.: Planktonic foraminifers as tracers of ocean-climate history, Ph.D. Thesis, Amsterdam, Free University Press, 346 pp., 1988.

## First-order estimate of the planktic foraminifer biomass

R. Schiebel and  
A. Movellan

Title Page

Abstract

Instruments

Data Provenance & Structure

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## First-order estimate of the planktic foraminifer biomass

R. Schiebel and  
A. Movellan

Title Page

Abstract

Instruments

Data Provenance & Structure

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



- Caron, D. A. and Bé, A. W. H.: Predicted and observed feeding rates of the spinose planktonic foraminifer *Globigerinoides sacculifer*, *B. Mar. Sci.*, 35, 1–10, 1984.
- Clayton, C. R. I., Abbireddy, C. O. R., and Schiebel, R.: A method of estimating the form of coarse particulates, *Geotechnique*, 59, 493–501, doi:10.1680/geot.2007.00195, 2009.
- 5 Dietrich, G., Kalle, K., Krauss, W., and Siedler, G.: *Allgemeine Meereskunde*, 3, Auflage, Gebrüder Bornträger, Berlin, Stuttgart, 593 pp., 1975.
- Hemleben, C., Spindler, M., and Anderson, O. R.: *Modern planktonic Foraminifera*, New York, Springer, 363 pp., 1989.
- 10 Itou, M., Ono, T., Oba, T., and Noriki, S.: Isotopic composition and morphology of living *Globobulimina scitula*: a new proxy of sub-intermediate ocean carbonate chemistry, *Mar. Micropaleontol.*, 42, 189–210, 2001.
- Kuroyanagi, A. and Kawahata, H.: Vertical distribution of living planktonic foraminifera in the seas around Japan, *Mar. Micropaleontol.*, 53, 173–196, 2004.
- 15 Leblanc, K., Arístegui, J., Armand, L., Assmy, P., Beker, B., Bode, A., Breton, E., Cornet, V., Gibson, J., Gosselin, M.-P., Kopczynska, E., Marshall, H., Peloquin, J., Piontkovski, S., Poulton, A. J., Quéguiner, B., Schiebel, R., Shipe, R., Stefels, J., van Leeuwe, M. A., Varela, M., Widdicombe, C., and Yallop, M.: A global diatom database – abundance, biovolume and biomass in the world ocean, *Earth Syst. Sci. Data Discuss.*, 5, 147–185, doi:10.5194/essdd-5-147-2012, 2012.
- 20 Lombard, F., Labeyrie, L., Michel, E., Bopp, L., Cortijo, E., Retailleau, S., Howa, H., and Jorissen, F.: Modelling planktic foraminifer growth and distribution using an ecophysiological multi-species approach, *Biogeosciences*, 8, 853–873, doi:10.5194/bg-8-853-2011, 2011.
- Loncaric, N., Peeters, F. J. C., Kroon, D., and Brummer, G. J. A.: Oxygen isotope ecology of recent planktic foraminifera at the central Walvis Ridge (SE Atlantic), *Paleoceanography*, 21, PA3009, doi:10.1029/2005PA001207, 2006.
- 25 Longhurst, A. R.: *Ecological Geography of the Sea*, 2nd Edn., Academic Press, 560 pp., 2007.
- Luo, Y.-W., Doney, S. C., Anderson, L. A., Benavides, M., Bode, A., Bonnet, S., Boström, K. H., Böttjer, D., Capone, D. G., Carpenter, E. J., Chen, Y. L., Church, M. J., Dore, J. E., Falcón, L. I., Fernández, A., Foster, R. A., Furuya, K., Gómez, F., Gundersen, K., Hynes, A. M., Karl, D. M., Kitajima, S., Langlois, R. J., LaRoche, J., Letelier, R. M., Marañón, E., McGillicuddy Jr., D. J., Moisanter, P. H., Moore, C. M., Mouriño-Carballido, B., Mulholland, M. R., Needoba, J. A., Orcutt, K. M., Poulton, A. J., Raimbault, P., Rees, A. P., Riemann, L., Shiozaki, T., Subramaniam, A., Tyrrell, T., Turk-Kubo, K. A., Varela, M., Villareal, T. A., Webb, E. A., White,

## First-order estimate of the planktic foraminifer biomass

R. Schiebel and  
A. Movellan

Title Page

Abstract

Instruments

Data Provenance & Structure

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

A. E., Wu, J., and Zehr, J. P.: Database of diazotrophs in global ocean: abundances, biomass and nitrogen fixation rates, *Earth Syst. Sci. Data Discuss.*, 5, 47–106, doi:10.5194/essdd-5-47-2012, 2012.

5 Michaels, A. F., Caron, D. A., Swanberg, N. R., Howse, F. A., and Michaels, C. M.: Planktonic sarcodines (Acantharia, Radiolaria, Foraminifera) in surface waters near Bermuda: abundance, biomass and vertical flux, *J. Plankton Res.*, 17, 131–163, 1995.

Milliman, J. D. and Droxler, A. W.: Neritic and pelagic carbonate sedimentation in the marine environment: Ignorance is not bliss, *Geol. Rundsch.*, 85, 496–504, 1996.

10 Mojtahid, M., Zubkov, M., Hartmann, M., and Gooday, A.: Grazing of intertidal benthic foraminifera on bacteria: Assessment using pulse-chase radiotracing, *J. Exp. Mar. Biol. Ecol.*, 399, 25–34, 2011.

Movellan, A., Schiebel, R., Zubkov, M. V., Smyth, A., and Howa, H.: Quantification of protein biomass of individual foraminifers using nano-spectrophotometry, *Biogeosciences Discuss.*, in preparation, 2012.

15 Obata, A., Ishizaka, J., and Endoh, M.: Global verification of critical depth theory for phytoplankton bloom with climatological in situ temperature and satellite ocean color data, *J. Geophys. Res.*, 101, 20657–20667, 1996.

Ortiz, J. D., Mix, A. C., and Collier, R. W.: Environmental control of living symbiotic and asym-biotic Foraminifera of the California Current, *Paleoceanography*, 10, 987–1009, 1995.

20 Peeters, F. J. C. and Brummer, G.-J. A.: The seasonal and vertical distribution of living planktic foraminifera in the NW Arabian Sea, *Geol. Soc. Spec. Publ.*, 195, 463–497, doi:10.1144/GSL.SP.2002.195.01.26, 2002.

Peeters, F., Ivanova, E., Conan, S., Brummer, G.-J., Ganssen, G., Troelstra, S., and van Hinte, J.: A size analysis of planktic foraminifera from the Arabian Sea, *Mar. Micropaleontol.*, 36, 31–63, 1999.

25 Retailleau, S., Howa, H., Schiebel, R., Lombard, F., Eynaud, F., Schmidt, S., Jorissen, F., and Labeyrie, L.: Planktic foraminiferal production along an offshore-onshore transect in the south-eastern Bay of Biscay, *Cont. Shelf Res.*, 29, 1123–1135, doi:10.1016/j.csr.2008.12.021, 2009.

30 Retailleau, S., Schiebel, R., and Howa, H.: Population dynamics of living planktic foraminifers in the hemipelagic southeastern Bay of Biscay, *Mar. Micropaleontol.*, 80, 89–100, 2011.

Schiebel, R.: Planktic foraminiferal sedimentation and the marine calcite budget, *Global Biogeochem. Cy.*, 16, 1065, doi:10.1029/2001GB001459, 2002.

## First-order estimate of the planktic foraminifer biomass

R. Schiebel and  
A. Movellan

Title Page

Abstract

Instruments

Data Provenance & Structure

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Schiebel, R. and Hemleben, C.: Interannual variability of planktic foraminiferal populations and test flux in the eastern North Atlantic Ocean (JGOFS), *Deep-Sea Res. Pt. II*, 47, 1809–1852, 2000.

Schiebel, R. and Hemleben, Ch.: Modern Planktic Foraminifera, *Palaeont. Z.*, 79, 135–148, 2005.

Schiebel, R., Hiller, B., and Hemleben, C.: Impacts of storms on recent planktic foraminiferal test production and CaCO<sub>3</sub> flux in the North Atlantic at 47° N, 20° W (JGOFS), *Mar. Micropaleontol.*, 26, 115–129, 1995.

Schiebel, R., Waniek, J., Bork, M., and Hemleben, C.: Planktic foraminiferal production stimulated by chlorophyll redistribution and entrainment of nutrients, *Deep-Sea Res. Pt. I*, 48, 721–740, 2001.

Schmuker, B. and Schiebel, R.: Spatial and temporal distribution of planktic foraminifers in the eastern Caribbean, *Mar. Micropaleontol.*, 46, 387–403, 2002.

Siccha, M., Schiebel, R., Howa, H., and Schmidt, S.: Short-term and small scale variability in planktic foraminifera test flux rates in the Bay of Biscay, *Deep-Sea Res. Pt. I*, 64, 146–156, 2012.

Smith, P., Krohn, R., Hermanson, G., Mallia, A., Provenzano, M., Fujimoto, E., Goeke, N., Olson, B. J., and Klenk, D.: Measurement of protein using bicinchoninic acid, *Anal. Biochem.*, 150, 76–85, 1985.

Spindler, M. and Dieckmann, G. S.: Distribution and abundance of the planktic foraminifer *Neogloboquadrina pachyderma* in sea ice of the Weddell Sea (Antarctica), *Polar Biol.*, 5, 185–191, 1986.

Spindler, M., Hemleben, C., Salomons, J. B., and Smit, L. P.: Feeding-behavior of some planktonic foraminifers in laboratory cultures, *J. Foramin. Res.*, 14, 1–3, 1984.

Vincent, E. and Berger, W. H.: Planktonic Foraminifera and their use in paleoceanography. *The Oceanic Lithosphere*, in: *The Sea*, edited by: Emiliani, C., 7, 1025–1119, 1981.

Volkman, R.: Planktic foraminifers in the outer Laptev Sea and Fram Strait – modern distribution and ecology, *J. Foramin. Res.*, 30, 157–176, 2000.

Weyl, P. K.: Micropaleontology and the ocean surface climate, *Science*, 202, 475–481, 1978.

Yoder, J. A., McClain, C. R., Feldman, G. C., and Esaias, W. E.: Annual cycles of phytoplankton chlorophyll concentrations in the global ocean: a satellite view, *Global Biogeochem. Cy.*, 7, 181–193, 1993.

Zubkov, M. V. and Sleigh, M. A.: Growth of Amoebae and Flagellates on Bacteria Deposited on Filters, *Microb. Ecol.*, 37, 107–115, 1999.

Zubkov, M. V., Fuchs, B. M., Eilers, H., Burkill, P. H., and Amann, R.: Determination of Total Protein Content of Bacterial Cells by SYPRO Staining and Flow Cytometry, *Appl. Environ. Microb.*, 65, 3251–3257, 1999.

5

# ESSDD

5, 243–280, 2012

## First-order estimate of the planktic foraminifer biomass

R. Schiebel and  
A. Movellan

Title Page

Abstract

Instruments

Data Provenance & Structure

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



First-order estimate of the planktic foraminifer biomass

R. Schiebel and A. Movellan

Title Page

Abstract Instruments

Data Provenance & Structure

Tables Figures

◀ ▶

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

**Table 1.** Summary of 1057 data points for population dynamics of live planktic foraminifers (>125 μm) m<sup>-3</sup>, used for the calculation of assemblage biomass. Each data point consists of five test size fraction of planktic foraminifers classified at the species level. All data are available from www.pangaea.de (Schiebel, 2002). Samples around 47° N/20° W (BIOTRANS Station) in the North Atlantic, and in the Arabian Sea were obtained within the JGOFS Program.

Cruise	Year	Month	Location	Lat. (° N)	Long. (° W/° E)	Water Depth (m)	No. of Samples
R/V <i>Meteor</i> 10/1	1989	April	N Atlantic	18.5	30.5° W	100–500	3
R/V <i>Meteor</i> 12/3	1990	June	N Atlantic	47–47.5	19.5–20° W	0–500	26
R/V <i>Meteor</i> 21/1	1992	March–April	N Atlantic	47	19.5° W	0–2500	62
R/V <i>Meteor</i> 21/2	1992	April–May	N Atlantic	47	19.5° W	0–2500	89
R/V <i>Meteor</i> 21/3	1992	May	N Atlantic	47–47.5	19.5–20° W	0–2500	18
R/V <i>Meteor</i> 21/3	1992	May	N Atlantic	57.5	20° W	0–700	9
R/V <i>Meteor</i> 21/5	1992	July	N Atlantic	67–72.5	8.5° W–3° E	0–2500	62
R/V <i>Poseidon</i> 200/6	1993	June	N Atlantic	44.8	19.8° W	0–100	5
R/V <i>Meteor</i> 26/1	1993	September	N Atlantic	47.8	19.8° W	0–2000	12
R/V <i>Meteor</i> 27/2	1994	January	N Atlantic	47–47.5	17.5–18.5° W	0–2500	18
R/V <i>Meteor</i> 36/2	1996	June	N Atlantic	33	22° W	60–80	1
R/V <i>Meteor</i> 36/5	1996	September	N Atlantic	46–48.5	17.5–22.3° W	0–2500	176
R/V <i>Meteor</i> 36/6	1996	October	N Atlantic	47.2	19.5° W	0–2500	26
FC <i>Archipelago</i> 3/97	1997	August	N Atlantic	32–35	29.2–31.7° W	0–1500	26
R/V <i>Poseidon</i> 231/3	1997	August	N Atlantic	33–36	22–30.8° W	0–2500	23
R/V <i>Meteor</i> 42/3	1998	August	N Atlantic	32.1–36	28.9–31.6° W	0–2500	51
R/V <i>Poseidon</i> 247/2	1999	January	N Atlantic	32.1–35.8	20.5–31.6° W	0–2500	91
R/V <i>Meteor</i> 35/1	1996	April–May	Caribbean	12–19	61.2–79.2° W	0–2500	129
R/V <i>Meteor</i> 31/2	1995	February–March	Red Sea	15.5–27.6	34.5–41.7° E	0–700	50
R/V <i>Meteor</i> 31/3	1995	March	Arabian Sea	16.2	59.7° E	0–2500	32
R/V <i>Meteor</i> 32/2	1995	May	Arabian Sea	3	65° E	0–2500	13
R/V <i>Meteor</i> 32/5	1995	August	Arabian Sea	17.1	60° E	0–100	5
R/V <i>Meteor</i> 33/1	1995	September–October	Arabian Sea	10–16.1	60.5–68.5° E	0–2500	53
R/V <i>Sonne</i> 117	1997	March	Arabian Sea	10–16.3	60.3–65° E	0–2500	26
R/V <i>Sonne</i> 118	1997	April–May	Arabian Sea	10–16.2	60.2–65° E	0–2500	26
R/V <i>Sonne</i> 119	1997	May–June	Arabian Sea	10–20.5	58.5–65° E	0–2500	25



**Table 2.** Summary of 754 specimens of 21 planktic foraminifer taxa, ontogenetic stages (*O. universa*), and 30 un-identified specimens analysed for their protein biomass from three cruises.

Cruise	Year	Month	Location	Water Depth (m)	Taxa	No. of Specimens
R/V Meteor 84/5	2011	June	Bay of Biscay	0–100	<i>Borbulina</i> sp.	1
R/V Meteor 84/5	2011	June	Bay of Biscay	0–100	<i>Globigerina bulloides</i>	57
R/V Tansei-Maruk KT11-20	2011	August	NW Pacific	0–500	<i>Globigerina bulloides</i>	7
R/V Meteor 84/5	2011	June	Bay of Biscay	0–100	<i>Globigerina falconensis</i>	2
R/V Poseidon 349	2007	April	Azores	500–700	<i>Globigerinella calida</i>	1
R/V Meteor 84/5	2011	June	Bay of Biscay	0–100	<i>Globigerinella siphonifera</i>	3
R/V Poseidon 349	2007	April	Azores	100–1500	<i>Globigerinella siphonifera</i>	7
R/V Meteor 84/5	2011	June	Bay of Biscay	0–100	<i>Globigerinita glutinata</i>	7
R/V Poseidon 349	2007	April	Azores	0–700	<i>Globigerinita glutinata</i>	6
R/V Meteor 84/5	2011	June	Bay of Biscay	0–100	<i>Globigerinita uvula</i>	10
R/V Meteor 84/5	2011	June	Bay of Biscay	0–100	<i>Globigerinoides sacculifer</i>	20
R/V Poseidon 349	2007	April	Azores	500–700	<i>Globigerinoides sacculifer</i>	1
R/V Meteor 84/5	2011	June	Bay of Biscay	0–100	<i>Globigerinoides trilobus</i>	4
R/V Tansei-Maruk KT11-20	2011	August	NW Pacific	80–200	<i>Globigerinoides trilobus</i>	1
R/V Meteor 84/5	2011	June	Bay of Biscay	0–50	<i>Globorotalia hirsuta</i>	1
R/V Poseidon 349	2007	April	Azores	100–1000	<i>Globorotalia hirsuta</i>	46
R/V Meteor 84/5	2011	June	Bay of Biscay	0–100	<i>Globorotalia inflata</i>	69
R/V Tansei-Maruk KT11-20	2011	August	NW Pacific	0–500	<i>Globorotalia inflata</i>	8
R/V Poseidon 349	2007	April	Azores	100–1500	<i>Globorotalia scitula</i>	26
R/V Poseidon 349	2007	April	Azores	100–700	<i>Globorotalia truncatulinoides</i>	14
R/V Meteor 84/5	2011	June	Bay of Biscay	0–100	<i>Hastigerina pelagica</i>	31
R/V Poseidon 349	2007	April	Azores	0–700	<i>Hastigerina pelagica</i>	15
R/V Meteor 84/5	2011	June	Bay of Biscay	0–100	<i>Neogloboquadrina dutertrei</i>	2
R/V Tansei-Maruk KT11-20	2011	August	NW Pacific	0–500	<i>Neogloboquadrina dutertrei</i>	8
R/V Meteor 84/5	2011	June	Bay of Biscay	0–100	<i>Neogloboquadrina incompta</i>	20
R/V Tansei-Maruk KT11-20	2011	August	NW Pacific	0–500	<i>Neogloboquadrina incompta</i>	120
R/V Poseidon 349	2007	April	Azores	200–300	<i>Neogloboquadrina incompta</i>	1
R/V Meteor 84/5	2011	June	Bay of Biscay	0–100	<i>Neogloboquadrina pachyderma</i>	42
R/V Tansei-Maruk KT11-20	2011	August	NW Pacific	0–500	<i>Neogloboquadrina pachyderma</i>	45
R/V Meteor 84/5	2011	June	Bay of Biscay	0–100	planktic foraminifer	9
R/V Tansei-Maruk KT11-20	2011	August	NW Pacific	0–200	planktic foraminifer	21
R/V Poseidon 349	2007	April	Azores	0–700	<i>Orbulina universa</i>	12
R/V Meteor 84/5	2011	June	Bay of Biscay	0–100	<i>Orbulina universa</i> (pre-spherical)	14
R/V Meteor 84/5	2011	June	Bay of Biscay	0–100	<i>Orbulina universa</i> (spherical)	57
R/V Meteor 84/5	2011	June	Bay of Biscay	0–100	p/d-intergrade	30
R/V Meteor 84/5	2011	June	Bay of Biscay	1.5	<i>Tenuitella fleisherii</i>	1
R/V Meteor 84/5	2011	June	Bay of Biscay	0–100	<i>Turborotalita quinqueloba</i>	30
R/V Tansei-Maruk KT11-20	2011	August	NW Pacific	0–200	<i>Turborotalita quinqueloba</i>	5

First-order estimate of the planktic foraminifer biomass

R. Schiebel and A. Movellan

Title Page

Abstract Instruments

Data Provenance & Structure

Tables Figures

◀ ▶

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion





## First-order estimate of the planktic foraminifer biomass

R. Schiebel and  
A. Movellan

**Table 3.** Average protein-biomass (arithmetic mean) per planktic foraminifer test-size bin ( $>100\ \mu\text{m}$ ), average frequency of specimens per size bin after Schiebel and Hemleben (2000), and protein content per size bin assuming average planktic foraminifer frequency.

Size bin ( $\mu\text{m}$ )	Average Protein Biomass ( $\mu\text{g}$ )	Average Frequency (%)	Biomass ( $\mu\text{g}$ ) per size bin
>100–125	0.700	50	0.35
>125–150	0.700	25	0.175
>150–200	0.838	12.5	0.10475
>200–250	0.982	6.25	0.061375
>250–315	1.540	3.125	0.048125
>315–400	2.627	1.6	0.042032
>400–500	3.416	0.8	0.027328
>500	9.152	0.4	0.036608
Total		99.675	0.845218

[Title Page](#)
[Abstract](#)
[Instruments](#)
[Data Provenance & Structure](#)
[Tables](#)
[Figures](#)
[⏪](#)
[⏩](#)
[◀](#)
[▶](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)


First-order estimate of the planktic foraminifer biomass

R. Schiebel and A. Movellan

Title Page

Abstract Instruments

Data Provenance & Structure

Tables Figures

⏪ ⏩

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

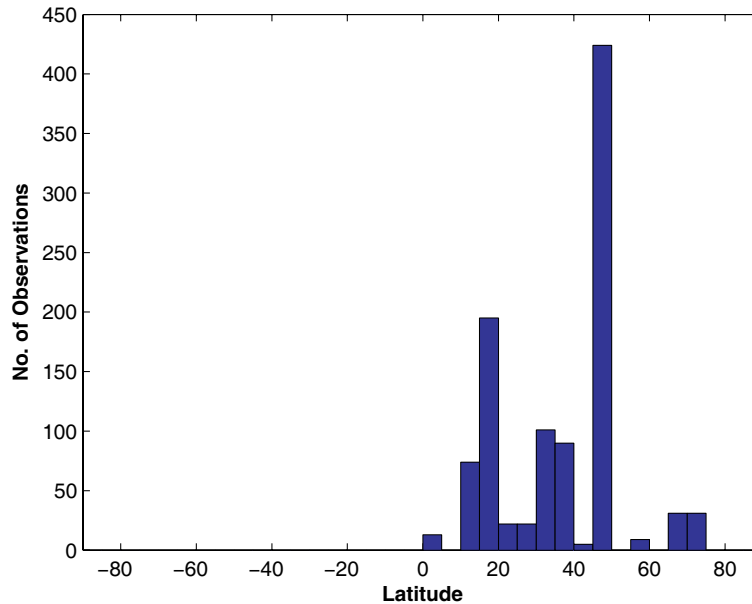
Discussion Paper | Discussion Paper | Discussion Paper | Discussion Paper | Discussion Paper

**Table 4.** Average (arithmetic mean and geometric mean) planktic foraminifer (>125 μm) protein biomass m<sup>-3</sup>, and integrated over water depth intervals (m<sup>-2</sup>) from arithmetic mean. Zero values excluded, n = 1017. Global annual biomass given for 322 × 10<sup>6</sup> km<sup>2</sup> and 9 month yr<sup>-1</sup>.

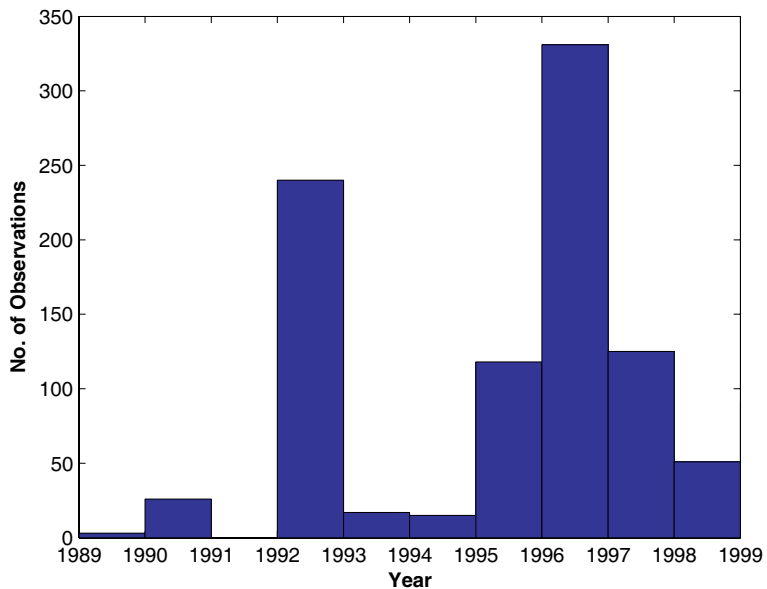
Water Depth (m)	Protein Biomass (μg m <sup>-3</sup> ) Arithmetic	Protein Biomass* (μg m <sup>-2</sup> )	Protein Biomass (μg m <sup>-3</sup> ) Geometric	Protein Biomass** (μg m <sup>-2</sup> )
0–20	70.04 (29.94–135.74)	1400.80	27.69	553.83
20–40	51.54 (22.50–85.82)	1030.77	20.07	401.32
40–60	51.09 (22.77–89.19)	1021.71	16.48	329.50
60–80	46.44 (16.74–84.69)	928.73	9.87	197.36
80–100	37.48 (12.29–66.26)	749.57	8.03	160.64
100–200	26.40 (7.34–44.51)	2640.20	3.90	390.14
200–300	11.16 (2.81–14.87)	1116.19	2.04	204.07
300–500	4.52 (1.34–5.00)	903.24	1.02	203.02
500–700	3.08 (0.89–3.32)	616.36	0.60	120.79
700–1000	0.96 (0.37–0.98)	289.03	0.39	117.83
1000–1500	0.42 (0.16–0.42)	208.71	0.18	92.28
1500–2000	0.34 (0.15–0.34)	169.20	0.16	81.40
2000–2500	0.38 (0.14–0.38)	190.62	0.16	81.93
<b>Total</b>		<b>11265.13</b>		<b>2934.11</b>
<b>Global (Tg C yr<sup>-1</sup>)</b>		<b>32.7 (11.1–51.3)</b>		<b>8.5</b>

\* from mean arithmetic mean, \*\* from geometric mean



**First-order estimate  
of the planktic  
foraminifer biomass**R. Schiebel and  
A. Movellan[Title Page](#)[Abstract](#)[Instruments](#)[Data Provenance & Structure](#)[Tables](#)[Figures](#)[⏪](#)[⏩](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

**Fig. 1.** Latitudinal distribution (Northern Hemisphere) of the planktic foraminifer assemblage data.  $n = 1057$ .



**Fig. 2.** Distribution of the planktic foraminifer assemblage data according to year.  $n = 1057$ .

## First-order estimate of the planktic foraminifer biomass

R. Schiebel and  
A. Movellan

[Title Page](#)

[Abstract](#) [Instruments](#)

[Data Provenance & Structure](#)

[Tables](#) [Figures](#)

[⏪](#) [⏩](#)

[◀](#) [▶](#)

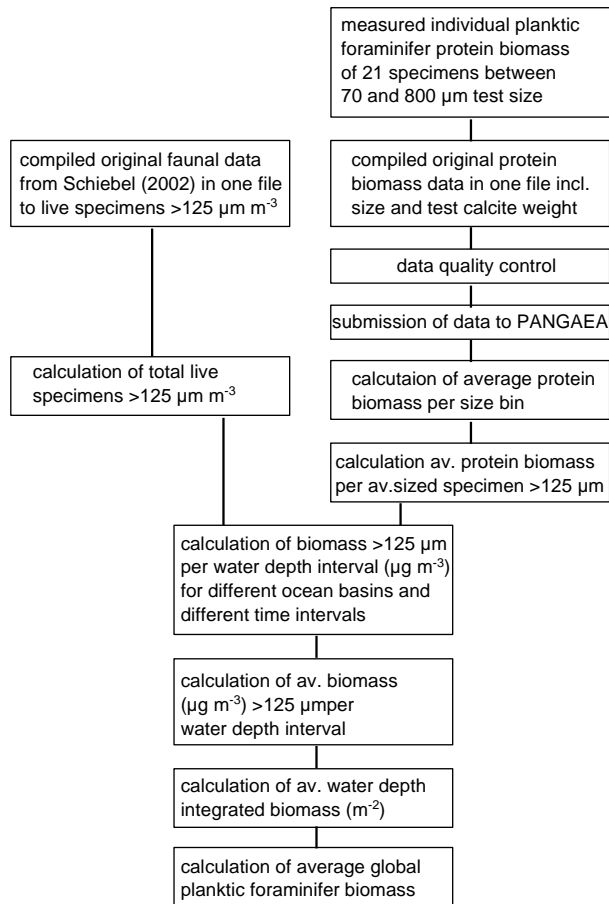
[Back](#) [Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

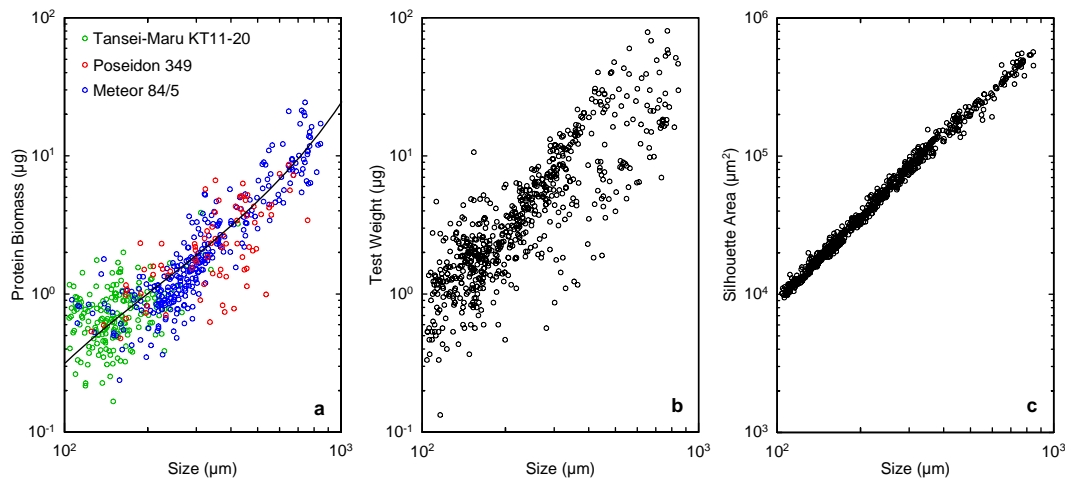




**Fig. 3.** Flow chart of the methodology used to construct a data set on planktic foraminifer biomass estimates from abundance data from [www.pangaea.de](http://www.pangaea.de) (see also, Schiebel, 2002), and individual species protein biomass data.

## First-order estimate of the planktic foraminifer biomass

R. Schiebel and  
A. Movellan



**Fig. 4.** (a) Variation of planktic foraminifer protein content with size (minimum diameter) at the Bay of Biscay (R/V *Meteor* 84/5), the Azores region (R/V *Poseidon* 349), and the western Pacific (R/V *Tansei-Maru* KT11-20).  $n = 561$ ,  $r^2 = 0.745$  (exponential fit),  $p < 0.00001$ , standard deviation of the residuals = 1.612. (b) Variation of test weight with size (minimum diameter) of the total data set ( $n = 646$ ). Different size-to-weight ratios of different species result in a low  $r^2 = 0.571$  (linear fit),  $p < 0.00001$ , standard deviation of the residuals = 6.623. (c) Relation of size (minimum diameter) and silhouette area, the latter of which has been shown to constrain size-and-weight changes to a high degree (Beer et al., 2010):  $n = 660$ ,  $r^2 = 0.974$ ,  $p < 0.00001$ .

Title Page

Abstract

Instruments

Data Provenance & Structure

Tables

Figures

◀

▶

◀

▶

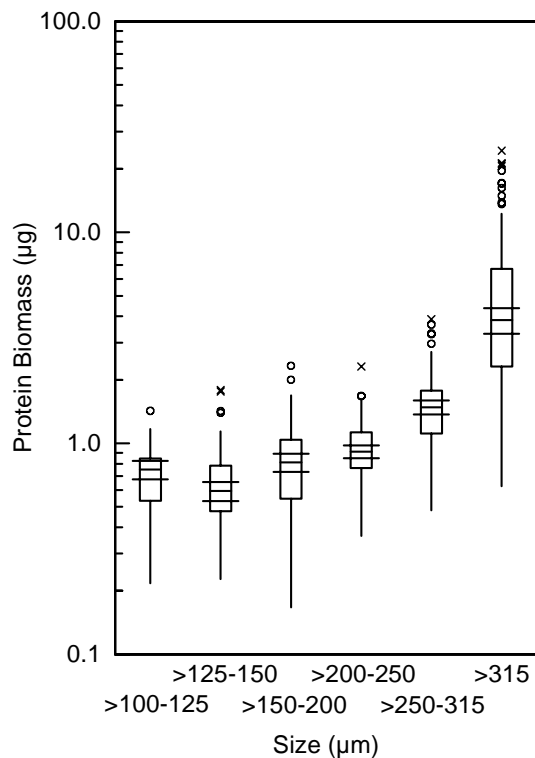
Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



**Fig. 5.** Average protein biomass versus minimum diameter displayed as median values, notches, and the upper and lower quartiles for the respective size bins. The arithmetic mean of protein biomass of the two smallest size bins is similar at 0.7 µg C per specimen. Circles and crosses indicate outside and far outside values, respectively.

**First-order estimate of the planktic foraminifer biomass**

R. Schiebel and A. Movellan

Title Page

Abstract Instruments

Data Provenance & Structure

Tables Figures

⏪ ⏩

◀ ▶

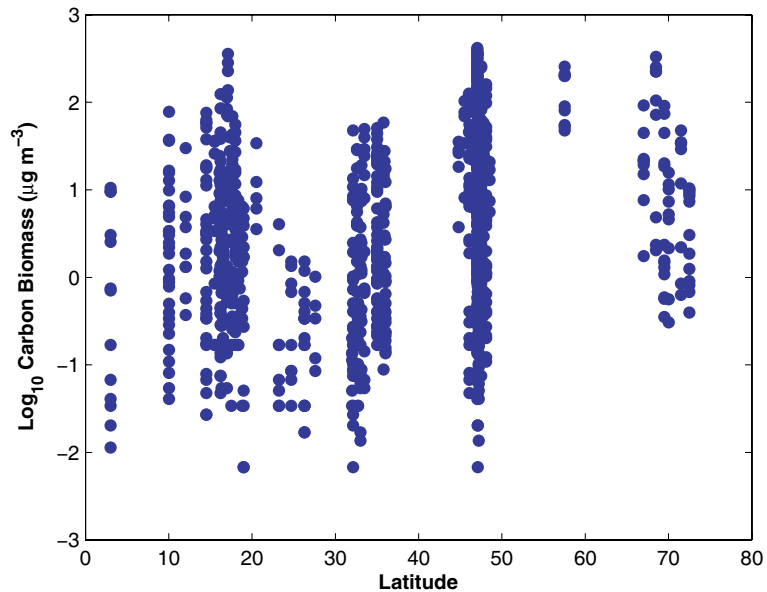
Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion





**Fig. 6.** Distribution of log-normalized planktic foraminifer cytoplasm-carbon biomass ( $\text{Log}_{10} \mu\text{g C m}^{-3}$ ) as a function of latitude ( $n = 1016$ ; without zero values).

**First-order estimate of the planktic foraminifer biomass**

R. Schiebel and  
A. Movellan

Title Page

Abstract Instruments

Data Provenance & Structure

Tables Figures

⏪ ⏩

◀ ▶

Back Close

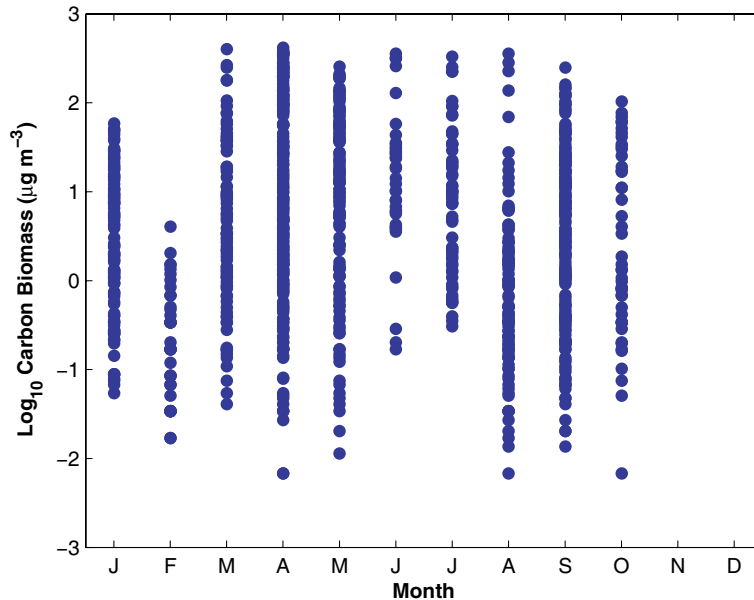
Full Screen / Esc

Printer-friendly Version

Interactive Discussion







**Fig. 7.** Distribution of log-normalized planktic foraminifer cytoplasm-carbon biomass ( $\text{Log}_{10} \mu\text{g C m}^{-3}$ ) as a function of time, i.e. months and Northern Hemisphere seasons ( $n = 1016$ ; without zero values).

**First-order estimate of the planktic foraminifer biomass**

R. Schiebel and A. Movellan

Title Page

Abstract Instruments

Data Provenance & Structure

Tables Figures

⏪ ⏩

⏴ ⏵

Back Close

Full Screen / Esc

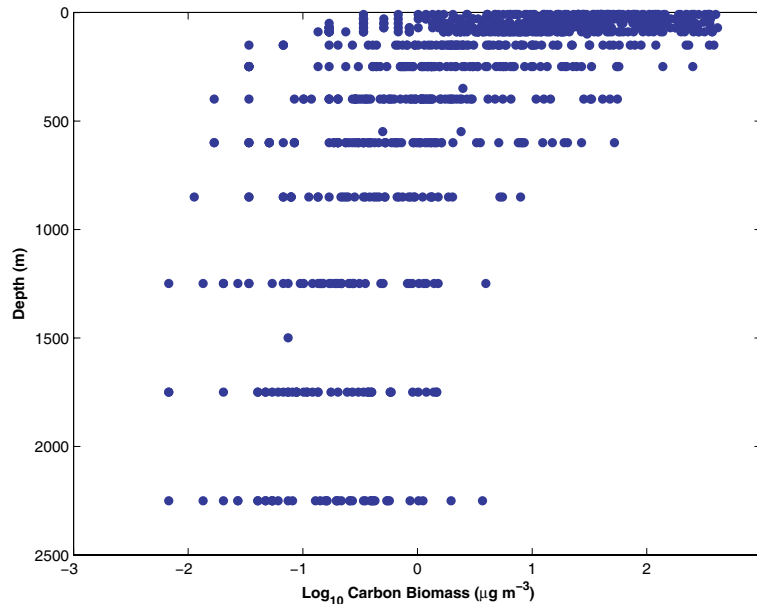
Printer-friendly Version

Interactive Discussion

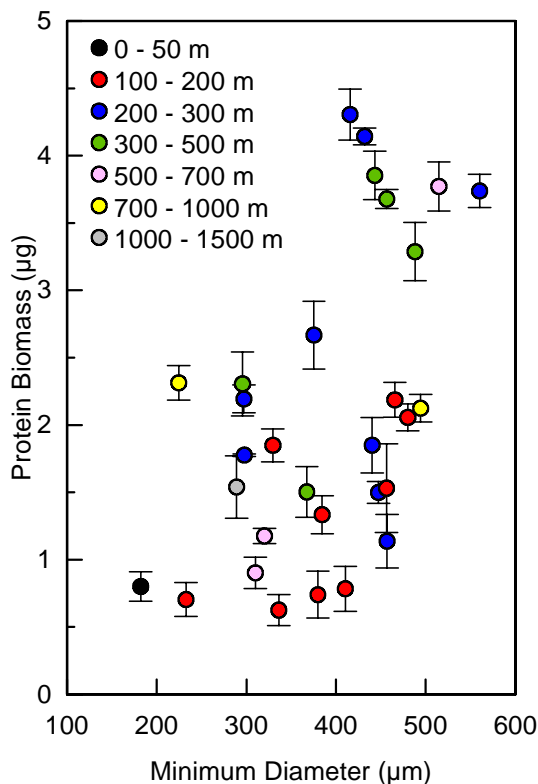


## First-order estimate of the planktic foraminifer biomass

R. Schiebel and  
A. Movellan

[Title Page](#)[Abstract](#)[Instruments](#)[Data Provenance & Structure](#)[Tables](#)[Figures](#)[⏪](#)[⏩](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

**Fig. 8.** Log-normalized carbon biomass ( $\text{Log}_{10} \mu\text{g m}^{-3}$ ) given for the total planktic foraminifer assemblage  $>125 \mu\text{m}$  (<http://doi.pangaea.de/10.1594/PANGAEA.777386>). Data are calculated from average individual protein-biomass data and faunal counts from the eastern North Atlantic, Caribbean, and Arabian Sea ( $n = 1016$ ; without zero values). All data given for the mid-points of the sampled water depth intervals. The assemblage protein biomass data of surface and deep waters cover about three orders of magnitude, and five orders of magnitude of variation in intermediate water depths (i.e. 100–500 m).



**Fig. 9.** Protein biomass of *Globorotalia hirsuta* from different water depth is largest between 200–700 m water depth, but is in general rather correlated to individual size ( $n = 30$ ). The largest individuals (adults) are known to dwell at subsurface depth. *Globorotalia hirsuta* has been selected for the analyses of depth dependant biomass changes because the species frequently occurs over a large water depth interval and are easily analysed for their protein content.

**First-order estimate of the planktic foraminifer biomass**

R. Schiebel and A. Movellan

Title Page

Abstract Instruments

Data Provenance & Structure

Tables Figures

⏪ ⏩

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## First-order estimate of the planktic foraminifer biomass

R. Schiebel and  
A. Movellan

Title Page

Abstract

Instruments

Data Provenance & Structure

Tables

Figures

◀

▶

◀

▶

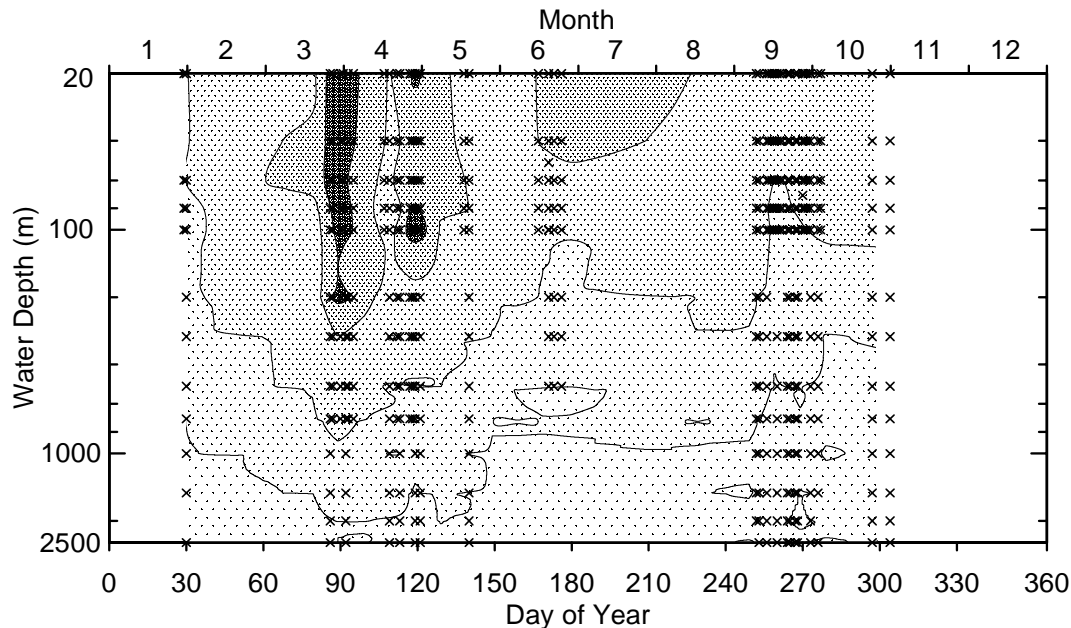
Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



**Fig. 10.** Average temporal development of planktic foraminifer assemblage  $>125\ \mu\text{m}$  protein biomass at BIOTRANS, North Atlantic at  $47^\circ\ \text{N}$ ,  $20^\circ\ \text{W}$ .  $n = 428$  data points (0–2500 m) between 1988 and 1996 (Table 1). Water depths refer to the lower limits of the sampled water depth intervals. Gray levels correspond to  $>200$ ,  $>100$ – $200$ ,  $>10$ – $100$ ,  $>1$ – $10$ ,  $>0$ – $1$ , and  $0\ \mu\text{g C m}^{-3}$ . White = time interval not sampled. Resolution:  $z = 20\ \text{m}$  water depth,  $t = 10$  days, using quadrant interpolation.

## First-order estimate of the planktic foraminifer biomass

R. Schiebel and  
A. Movellan

Title Page

Abstract

Instruments

Data Provenance & Structure

Tables

Figures

◀

▶

◀

▶

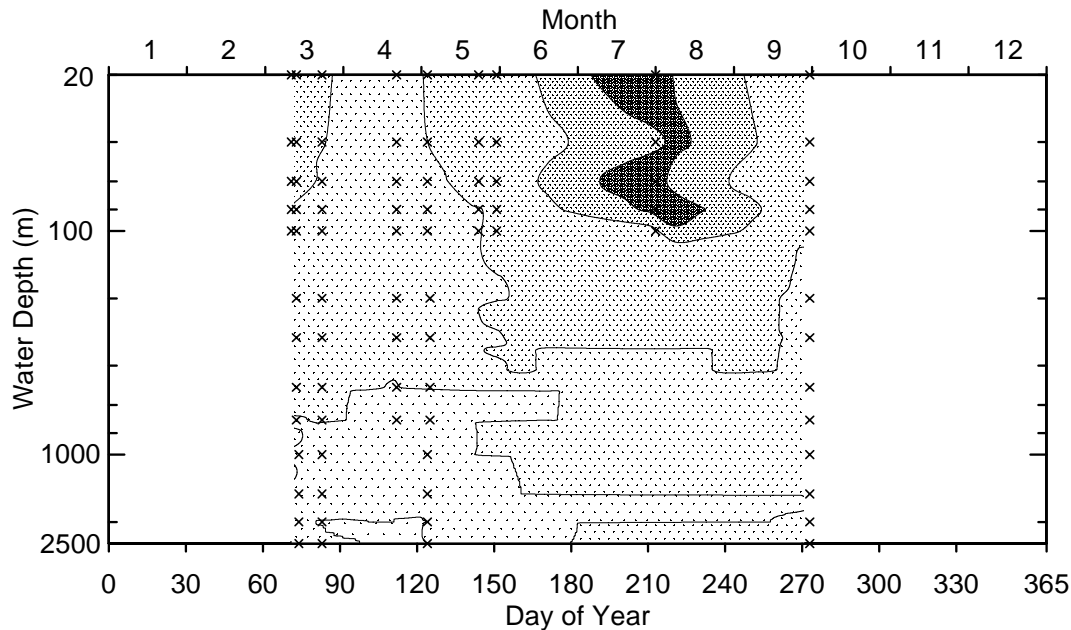
Back

Close

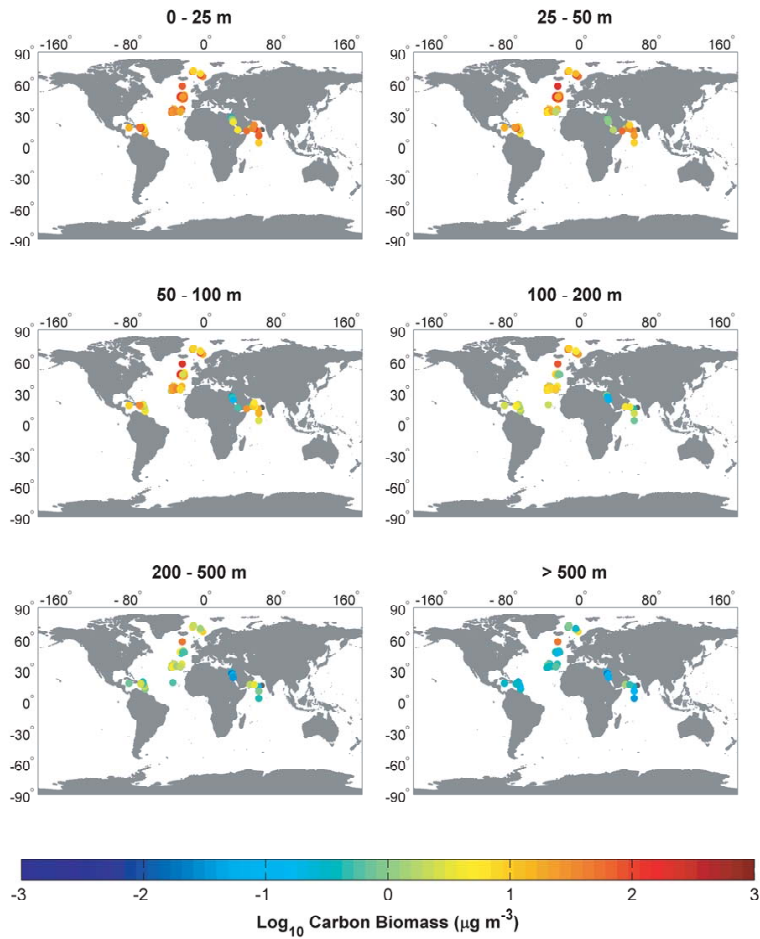
Full Screen / Esc

Printer-friendly Version

Interactive Discussion



**Fig. 11.** Average temporal protein biomass distribution of the planktic foraminifer assemblage  $>125 \mu\text{m}$  at WAST, Arabian Sea at  $20^\circ \text{N}$ ,  $60^\circ \text{E}$ .  $n = 81$  data points at 0–2500 m water depth, in 1995 and 1997 (Table 1). Water depths refer to the lower limits of the sampled water depth intervals. Gray levels correspond to  $>200$ ,  $>100\text{--}200$ ,  $>10\text{--}100$ ,  $>1\text{--}10$ ,  $>0\text{--}1$ , and  $0 \mu\text{g C m}^{-3}$ . White = time interval not sampled. Interpolated for at  $z = 20 \text{ m}$ , and  $t = 10 \text{ days}$ , using quadrant interpolation.



**Fig. 12.** Log-normalized average depth related PFAB (Log<sub>10</sub> µg C m<sup>-3</sup>) binned on a 3 × 3° grid, comprising the North Atlantic Ocean, Caribbean, Arabian Sea and Gulf of Aden, and Red Sea.

First-order estimate of the planktic foraminifer biomass

R. Schiebel and A. Movellan

Title Page

Abstract

Instruments

Data Provenance & Structure

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion