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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. With a new non-destructive protocol developed from the bicinchoninic acid (BCA) method and nano-photospectrometry, we have analysed the protein-biomass, along with test size and weight, of 754 individual planktic foraminifers from 21 different species and morphotypes. From additional CHN analysis, it can be assumed that protein-biomass equals carbon-biomass. Accordingly, the average individual planktic foraminifer protein- and carbon-biomass amounts to 0.845 μg. Samples include symbiont bearing and symbiont-barren species from the sea surface down to 2500 m water depth. Conversion factors between individual biomass and assemblage-biomass are calculated for test sizes between 72 and 845 μm (minimum test diameter). Assemblage-biomass data presented here include 1128 sites and water depth intervals. The regional coverage of data includes the North Atlantic, Arabian Sea, Red Sea, and Caribbean as well as literature data from the eastern and western North Pacific, and covers a wide range of oligotrophic to eutrophic waters over six orders of magnitude of planktic-foraminifer assemblage-biomass (PFAB). A first order estimate of the average global planktic foraminifer biomass production (> 125 μm) ranges from 8.2–32.7 Tg C yr^{-1} (i.e. 0.008–0.033 Gt C yr^{-1}), and might be more than three times as high including neanic and juvenile individuals adding up to 25–100 Tg C yr^{-1}. However, this is a first estimate of regional 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 http://www.pangaea.de (http://doi.pangaea.de/10.1594/PANGAEA.777386).

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 ocean, 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 ubiquitious. The 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; Volkmann, 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, such as monsoonal activity and upwelling intensity (Hemleben et al., 1989).

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 foraminiferal 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 specialised 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 diet is abundant. The prolocular ontogenetic stage consists of a first chamber built of calcite and ranges from 12–25 μm 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 the selection of diet (Brummer and Kroon, 1988). Adult specimens consist of 10–20 chambers, and tests are between 100 and 1000 μm in size (on average ~ 250 μm).

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 the of lipids and starch is stored in special vacuoles (Schiebel and Hemleben, 2005). Symbiont-bearing species depend on light and are bound to the euphotic layer, and subsurface to deep-dwelling species are symbiont-barren (e.g. Bé, 1982).

Although planktic foraminifers constitute only a minor portion of the total zooplankton, they are major producers of marine calcareous shells (called tests). Consequently, planktic foraminifers have been a 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 carbon-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 also present in our data set, and our new protein-biomass data are discussed to equal carbon-biomass. Conversion factors between carbon-biomass and volume range between 0.018 and 0.18 pg C μm^{-3} with an average of 0.089 ± 0.055 pg C μm^{-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 assemblage-biomass (PFAB; $\mu g\, C\, m^{-3}$) and biomass production ($Tg\, C\, yr^{-1}$) 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 as part of the German contribution to the Joint Global Ocean Flux Studies in the 1990s at stations and transects in the North Atlantic (BIOTRANS) and Arabian Sea repeatedly sampled at seasonal and regional resolution, over a wide range of global marine primary productivity from oligotrophic to eutrophic conditions. In addition, 71 datapoints on live planktic foraminifer assemblages (> 125 μm) are included from Ortiz et al. (1995) and Kuroyanagi and

Table 1. Summary of 1128 data points on population dynamics of live planktic foraminifers (> 125 μm) m^{-3}, used for the calculation of assemblage biomass. Each data point consists of five test size fractions 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/Ref.	Year	Month	Location	Lat. (° N)	Long. (° W/° E)	Water Depth (m)	No. of Samples
R/V *Meteor* 10/1	1989	April	N Atlantic	18.5	30.5° W	100–500	3
R/V *Meteor* 12/3	1990	June	N Atlantic	47–47.5	19.5–20° W	0–500	26
R/V *Meteor* 21/1	1992	March–April	N Atlantic	47	19.5° W	0–2500	62
R/V *Meteor* 21/2	1992	April–May	N Atlantic	47	19.5° W	0–2500	89
R/V *Meteor* 21/3	1992	May	N Atlantic	47–47.5	19.5–20° W	0–2500	18
R/V *Meteor* 21/3	1992	May	N Atlantic	57.5	20° W	0–700	9
R/V *Meteor* 21/5	1992	July	N Atlantic	67–72.5	8.5° W–3° E	0–2500	62
R/V *Poseidon* 200/6	1993	June	N Atlantic	44.8	19.8° W	0–100	5
R/V *Meteor* 26/1	1993	September	N Atlantic	47.8	19.8° W	0–2000	12
R/V *Meteor* 27/2	1994	January	N Atlantic	47–47.5	17.5–18.5° W	0–2500	18
R/V *Meteor* 36/2	1996	June	N Atlantic	33	22° W	60–80	1
R/V *Meteor* 36/5	1996	September	N Atlantic	46–48.5	17.5–22.3° W	0–2500	176
R/V *Meteor* 36/6	1996	October	N Atlantic	47.2	19.5° W	0–2500	26
FC *Archipelago* 3/97	1997	August	N Atlantic	32–35	29.2–31.7° W	0–1500	26
R/V *Poseidon* 231/3	1997	August	N Atlantic	33–36	22–30.8° W	0–2500	23
R/V *Meteor* 42/3	1998	August	N Atlantic	32.1–36	28.9–31.6° W	0–2500	51
R/V *Poseidon* 247/2	1999	January	N Atlantic	32.1–35.8	20.5–31.6° W	0–2500	91
R/V *Meteor* 35/1	1996	April–May	Caribbean	12–19	61.2–79.2° W	0–2500	129
R/V *Meteor* 31/2	1995	February–March	Red Sea	15.5–27.6	34.5–41.7° E	0–700	50
R/V *Meteor* 31/3	1995	March	Arabian Sea	16.2	59.7° E	0–2500	32
R/V *Meteor* 32/2	1995	May	Arabian Sea	3	65° E	0–2500	13
R/V *Meteor* 32/5	1995	August	Arabian Sea	17.1	60° E	0–100	5
R/V *Meteor* 33/1	1995	September–October	Arabian Sea	10–16.1	60.5–68.5° E	0–2500	53
R/V *Sonne* 117	1997	March	Arabian Sea	10–16.3	60.3–65° E	0–2500	26
R/V *Sonne* 118	1997	April–May	Arabian Sea	10–16.2	60.2–65° E	0–2500	26
R/V *Sonne* 119	1997	May–June	Arabian Sea	10–20.5	58.5–65° E	0–2500	25
Ortiz et al. (1995)	1990	September	NE Pacific	41.5–42.2	125.7–131.1° W	0–200	15
Kuroyanagi and Kawahata (2004)	2002	May–June	NW Pacific	32.2–41.6	131.7–143.4° E	0–200	56

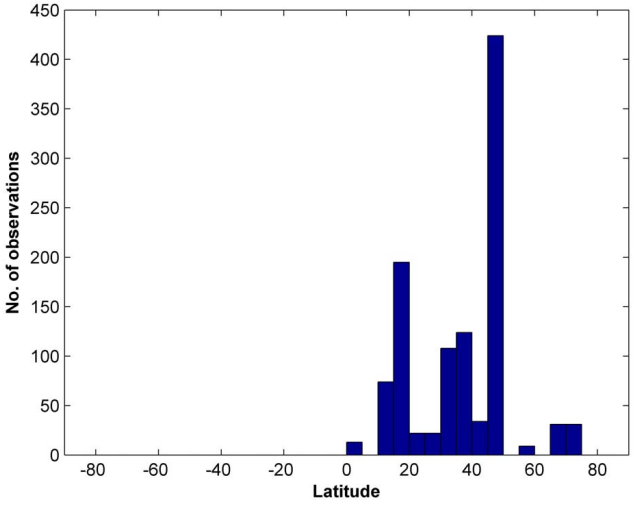

Figure 1. Latitudinal distribution (Northern Hemisphere) of the planktic foraminifer assemblage data. $n = 1128$.

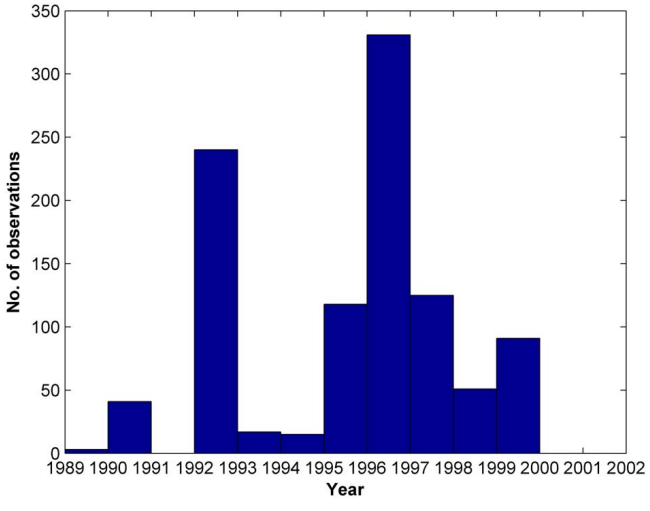

Figure 2. Distribution of the planktic foraminifer assemblage data according to year. $n = 1128$.

Table 2. Summary of 754 specimens of 21 planktic foraminifer taxa, ontogenetic stages (of *O. universa*), and 30 unidentified 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	*Biorbulina* sp.	1
R/V *Meteor* 84/5	2011	June	Bay of Biscay	0–100	*Globigerina bulloides*	57
R/V *Tansei-Maru* KT11-20	2011	August	NW Pacific	0–500	*Globigerina bulloides*	7
R/V *Meteor* 84/5	2011	June	Bay of Biscay	0–100	*Globigerina falconensis*	2
R/V *Poseidon* 349	2007	April	Azores	500–700	*Globigerinella calida*	1
R/V *Meteor* 84/5	2011	June	Bay of Biscay	0–100	*Globigerinella siphonifera*	3
R/V *Poseidon* 349	2007	April	Azores	100–1500	*Globigerinella siphonifera*	7
R/V *Meteor* 84/5	2011	June	Bay of Biscay	0–100	*Globigerinita glutinata*	7
R/V *Poseidon* 349	2007	April	Azores	0–700	*Globigerinita glutinata*	6
R/V *Meteor* 84/5	2011	June	Bay of Biscay	0–100	*Globigerinita uvula*	10
R/V *Meteor* 84/5	2011	June	Bay of Biscay	0–100	*Globigerinoides sacculifer*	20
R/V *Poseidon* 349	2007	April	Azores	500–700	*Globigerinoides sacculifer*	1
R/V *Meteor* 84/5	2011	June	Bay of Biscay	0–100	*Globigerinoides trilobus*	4
R/V *Tansei-Maru* KT11-20	2011	August	NW Pacific	80–200	*Globigerinoides trilobus*	1
R/V *Meteor* 84/5	2011	June	Bay of Biscay	0–50	*Globorotalia hirsuta*	1
R/V *Poseidon* 349	2007	April	Azores	100–1000	*Globorotalia hirsuta*	46
R/V *Meteor* 84/5	2011	June	Bay of Biscay	0–100	*Globorotalia inflata*	69
R/V *Tansei-Maru* KT11-20	2011	August	NW Pacific	0–500	*Globorotalia inflata*	8
R/V *Poseidon* 349	2007	April	Azores	100–1500	*Globorotalia scitula*	26
R/V *Poseidon* 349	2007	April	Azores	100–700	*Globorotalia truncatulinoides*	14
R/V *Meteor* 84/5	2011	June	Bay of Biscay	0–100	*Hastigerina pelagica*	31
R/V *Poseidon* 349	2007	April	Azores	0–700	*Hastigerina pelagica*	15
R/V *Meteor* 84/5	2011	June	Bay of Biscay	0–100	*Neogloboquadrina dutertrei*	2
R/V *Tansei-Maru* KT11-20	2011	August	NW Pacific	0–500	*Neogloboquadrina dutertrei*	8
R/V *Meteor* 84/5	2011	June	Bay of Biscay	0–100	*Neogloboquadrina incompta*	20
R/V *Tansei-Maru* KT11-20	2011	August	NW Pacific	0–500	*Neogloboquadrina incompta*	120
R/V *Poseidon* 349	2007	April	Azores	200–300	*Neogloboquadrina incompta*	1
R/V *Meteor* 84/5	2011	June	Bay of Biscay	0–100	*Neogloboquadrina pachyderma*	42
R/V *Tansei-Maru* KT11-20	2011	August	NW Pacific	0–500	*Neogloboquadrina pachyderma*	45
R/V *Meteor* 84/5	2011	June	Bay of Biscay	0–100	planktic foraminifer	9
R/V *Tansei-Maru* KT11-20	2011	August	NW Pacific	0–200	planktic foraminifer	21
R/V *Poseidon* 349	2007	April	Azores	0–700	*Orbulina universa*	12
R/V *Meteor* 84/5	2011	June	Bay of Biscay	0–100	*Orbulina universa* (pre-spherical)	14
R/V *Meteor* 84/5	2011	June	Bay of Biscay	0–100	*Orbulina universa* (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	*Tenuitella fleisheri*	1
R/V *Meteor* 84/5	2011	June	Bay of Biscay	0–100	*Turborotalita quinqueloba*	30
R/V *Tansei-Maru* KT11-20	2011	August	NW Pacific	0–200	*Turborotalita quinqueloba*	5

Kawahata (2004), from waters off Oregon (US) and Japan, respectively.

Planktic foraminifer protein-biomass was obtained from 754 individuals, including 21 species and morphotypes from all ontogenetic stages (Table 2). The average PFAB 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-μm and a rectangular opening of 0.25 m^2 (HYDROBIOS midi®) was applied for vertical hauls at 0.3–0.5 $m\,s^{-1}$ towing speed (cf. Schiebel et al., 1995). Standardized water depth intervals of 0-20-40-60-80-100-200-300-500-700-1000-1500-2000-2500 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 μm and > 315 μm

Table 3. Average protein-biomass (arithmetic mean) per planktic foraminifer test-size bin (> 100 µm), 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 (µm)	Average protein biomass (µg)	Average frequency (%)	Biomass (µg) 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

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 interannual data sets were combined, and regional data sets from different ocean basins 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 µm) of the plankton net, the faunal data analysed here ($n = 6100$) refer to the size fraction > 125 µm. Census data are available from the Pangaea database (Bremerhaven, Germany, www.pangaea.de).

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 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 analysed. From the R/V *Tansei-Maru* cruise KT11-20, 21–25 August 2011, in the Pacific off northeastern Honshu, Japan, 213 live foraminifers were analysed. 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 analysed from 18 sites and water depths ranging from 0 to 1500 m (Table 2). Specimens were classified and processed individually. Each

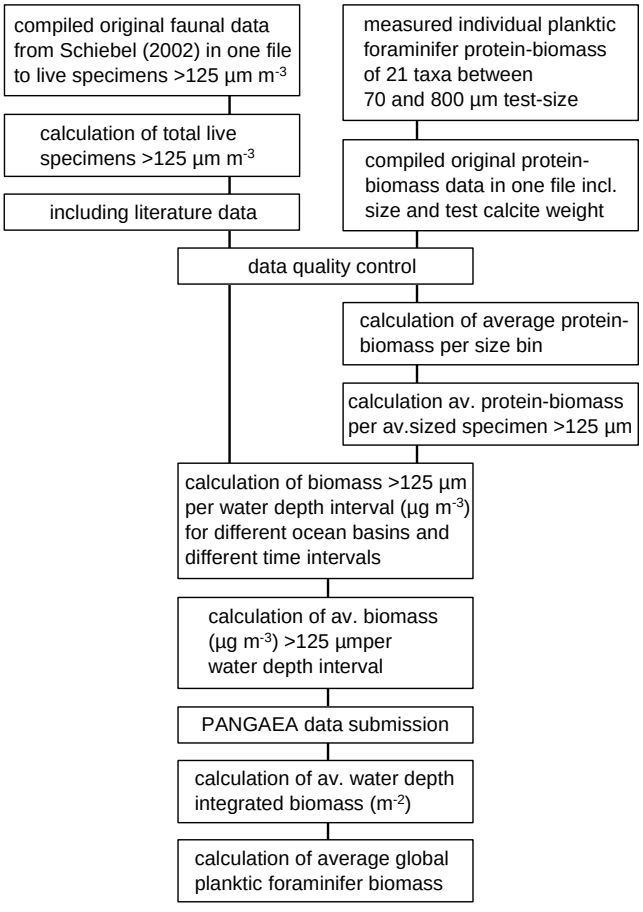

Figure 3. Flow chart of the methodology used to construct a data set on planktic foraminifer biomass estimates from abundance data from www.pangaea.de (Schiebel, 2002), Ortiz et al. (1995), Kuroyanagi and Kawahata (2004), and individual species protein-biomass data.

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 deionized water for less than a second to remove the seawater. Each foraminifer was individually stored in an Eppendorf cup, and frozen at −80 °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 (BCA) method developed by Smith (1985), using a mix of copper solution (4 % (w/v) $CuSO_4$ $5H_2O$ solution; Sigma-Aldrich) and BCA (Sigma) solution (Smith et al., 1985; Zubkov and Sleigh, 1999; Mojtahid et al., 2011). In contact with proteins the Cu^{2+} ions of

Table 4. Average (arithmetic mean and geometric mean) planktic foraminifer (> 125 μm) protein biomass m^{-3}, and integrated over water depth intervals (m^{-2}) from arithmetic mean, and annual biomass production (Tg C yr^{-1}). Zero values excluded, $n = 1087$. Global annual biomass production is given for 322×10^6 km^2 and 9 month yr^{-1}.

Water depth (m)	Protein biomass ($\mu g\ m^{-3}$) arithmetic	Protein biomass* ($\mu g\ m^{-2}$)	Protein biomass ($\mu g\ m^{-3}$) geometric	Protein biomass** ($\mu g\ m^{-2}$)
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
Total	– –	11 265.13	–	2934.11
Global (Tg C yr^{-1})	– –	32.7 (11.1–51.3)	–	8.5

* From mean arithmetic mean, ** from geometric mean.

the copper solution are reduced to Cu^+. The Cu^+ 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 albumin (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 (*Meteor* 84/5 and *Tansei-Maru* KT11-20), or after being unfrozen in the case of the R/V *Poseidon* 349 samples, 20 μl 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 seconds 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 the 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, and compared to specimens from the same populations, which were subjected to an osmotic shock (not crushed) for cytoplasm exposure.

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 micro-slides. Each test was photographed from the apertural side with an automated incident light microscope installed at the University of Angers, and driven by analySIS® software (Bollmann et al., 2004; Clayton et al., 2009), at a resolution of 1.4 μm^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 μg) was employed to weigh individual foraminifer tests.

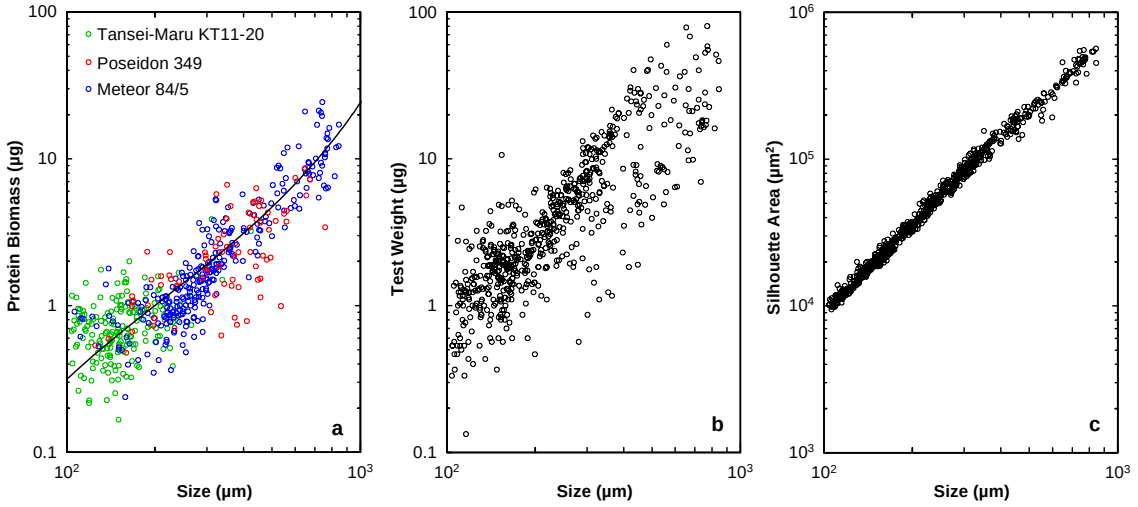

Figure 4. **(a)** Variation of planktic foraminifer protein content with size (minimum diameter) at the Bay of Biscay (R/V *Meteor* 84/5), the Azores region (R/V *Poseidon* 349), and the western Pacific (R/V *Tansei-Maru* KT11-20). $n = 561$, $r^2 = 0.745$ (exponential fit), $p < 0.00001$, standard deviation 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): $n = 660$, $r^2 = 0.974$, $p < 0.00001$.

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 ± 0.17 µg.

2.4 Quality control

Most of the data points on planktic-foraminifer assemblage-biomass (PFAB) presented here are calculated from own data on population dynamics (faunal data, standing stocks), and individual protein-biomass data. All of our own data points on standing stocks and 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 (6 out of 762). All zero values (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. 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. In addition to own data, we have carefully chosen literature data of similar sampling (i.e. gear, depth intervals, and live specimens > 125-µm test-size) and storing method (buffered formaldehyde). All of those criteria could be applied to the data of Kuroyanagi and Kawahata (2004) and Ortiz et al. (1995).

3 Results

3.1 Efficiency of the BCA method 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 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 of *G. scitula* was significantly larger for crushed specimens (average 2.416 µg) than for the specimens subjected to an osmotic shock (average 2.238 µg; $p = 0.02465$), 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 architecture and the small aperture of this small globorotalid species. The

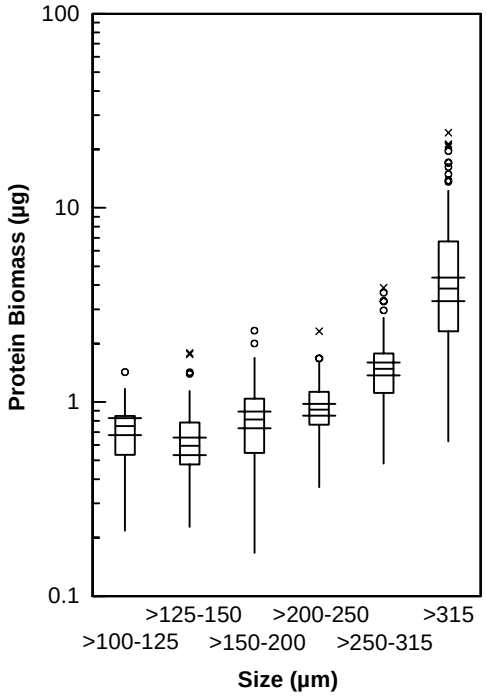

Figure 5. Average protein-biomass versus minimum diameter displayed as median values, notches, and the upper and lower quartiles for the respective size bins. The arithmetic mean of protein-biomass of the two smallest size bins is similar at 0.7 µg C per specimen. Circles and crosses indicate outside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

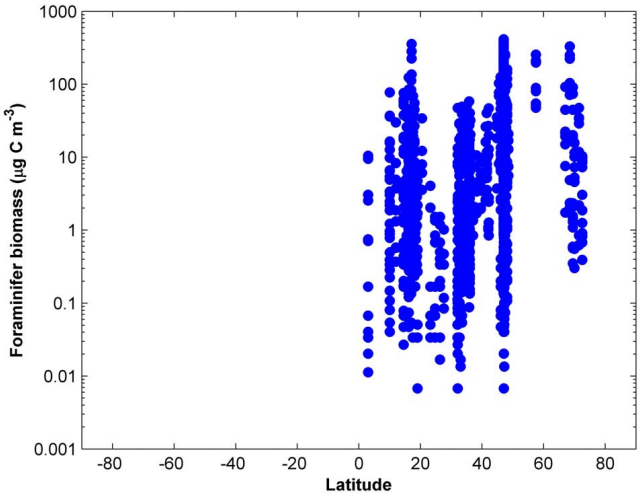

Figure 6. Distribution of log-normalised planktic foraminifer cytoplasm-carbon biomass (Log_{10} µg C m^{-3}) as a function of latitude (n = 1016; without zero values).

same might be true for the globorotalid species *G. truncatulinoides*. Since both species *G. scitula* and *G. truncatulinoides* 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). In turn, the size-normalised 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 protein-biomass of the two smallest planktic foraminifer test size bins > 100–125 µm and > 125–150 µm is similar at 0.7 µg per specimen (Table 3), and significantly ($t_{99\%}$) increases in the larger size bins (Table 3, Fig. 5). In turn, 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 average global individual planktic foraminifer protein-biomass is calculated at 0.845 µg (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 protein-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 protein-biomass of planktic foraminifers per square meter down to 2500 m water depth is 11.27 mg (Table 4).

The $CaCO_3$ 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 $CaCO_3$ mass of planktic foraminifer tests of 100.09 g mol^{-1}, and a calcite-carbon mass of 12.01 g mol^{-1}, the planktic foraminifer test calcite-carbon mass resembles ~ 36 % of the protein-biomass, but which is not included in the biomass data presented in the following.

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 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

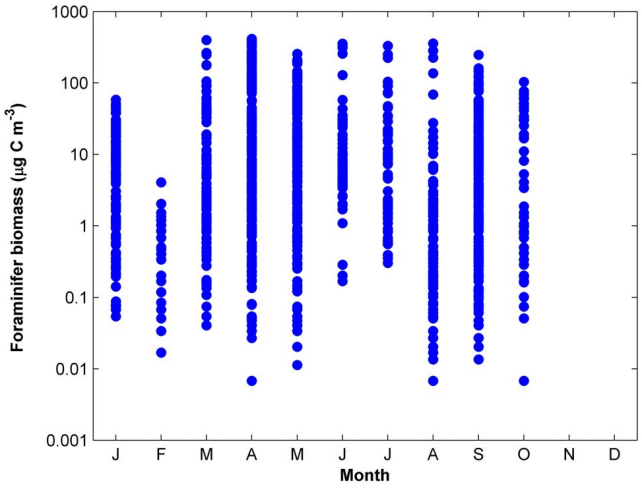

Figure 7. Distribution of log-normalised planktic foraminifer cytoplasm-carbon biomass (Log_{10} µg C m^{-3}) as a function of time, i.e. months and Northern Hemisphere seasons (n = 1087; without zero values).

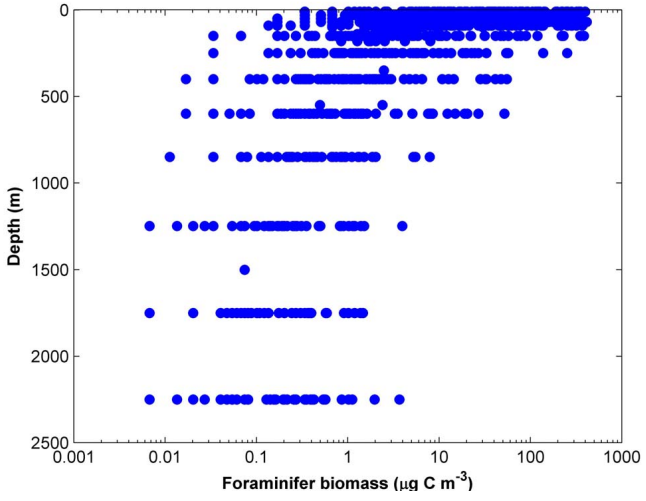

Figure 8. Log-normalised carbon-biomass (Log_{10} µg m^{-3}) given for the total planktic foraminifer assemblage > 125 µm (http://doi.pangaea.de/10.1594/PANGAEA.777386). Data are calculated from average individual protein-biomass data and faunal counts from the eastern North Atlantic, Caribbean, and Arabian Sea (n = 1087; 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).

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).

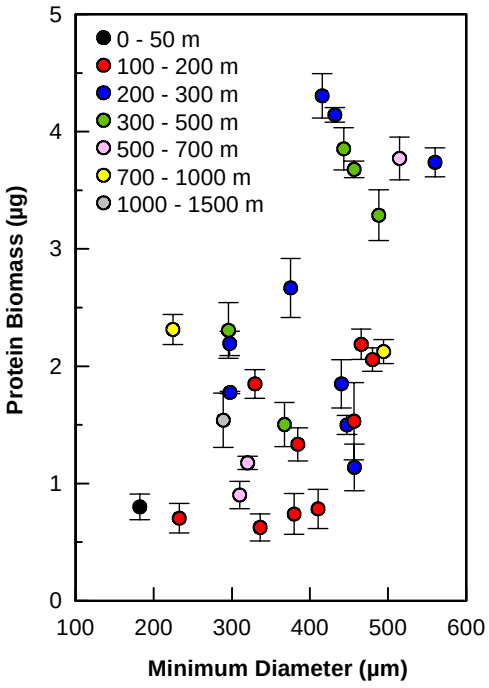

Figure 9. Protein-biomass of *Globorotalia hirsuta* from different water depth is largest between 200–700 m water depth, but is in general rather correlated to individual size (n = 30). The largest individuals (adults) are known to dwell at subsurface depth. *Globorotalia hirsuta* has been selected for 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.

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 the 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 µg m^{-3} at 68° N in July was quantitatively similar to that in spring at 47° N (Fig. 12). Highest PFAB concentration of > 100 µg 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). PFABs in the eastern and western Pacific range at medium values in comparison to PFABs in the Atlantic and Arabian Sea. 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).

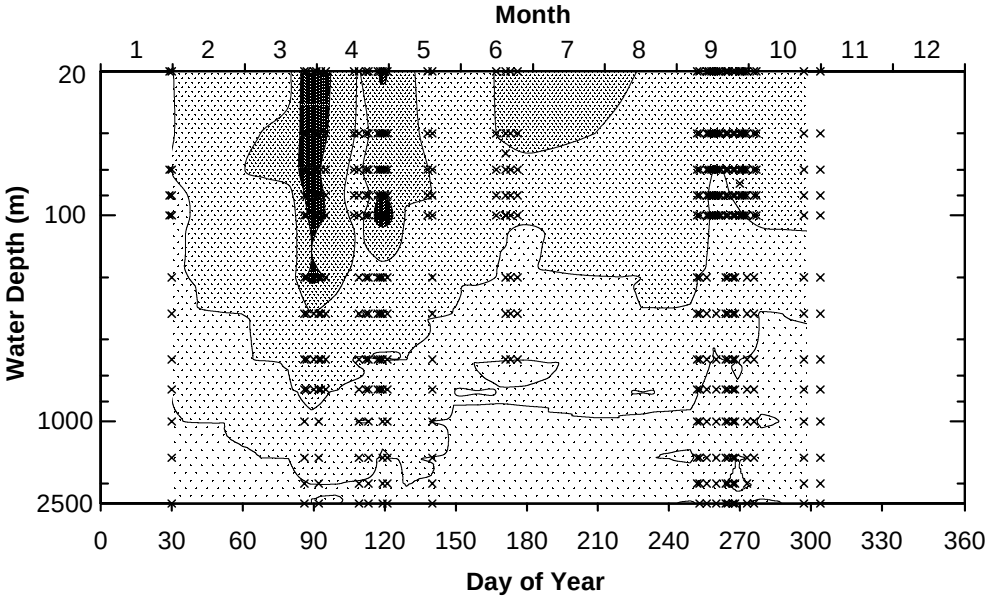

Figure 10. Average temporal development of planktic foraminifer assemblage > 125 μm protein-biomass at BIOTRANS, North Atlantic at 47° N, 20° W. $n = 428$ data points (0–2500 m) between 1990 and 1996 (Table 1). Water depths refer to the lower limits of the sampled water depth intervals. Grey levels correspond to > 200, > 100–200, > 10–100, > 1–10, > 0–1, and 0 μg C m^{-3}. White = time interval not sampled. Resolution: $z = 20$ m water depth, $t = 10$ days, using quadrant interpolation.

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 analysis. An average species of 315-μm minimum test diameter contains about 2.2 μg protein-biomass (Fig. 4a), which amounts to 2.2 μg per 10^5 μm^2 silhouette area (Fig. 4b), the latter being a reliable measure of the foraminifer test volume (Beer et al., 2010). The resulting conversion factor between biomass and volume of 0.092 ± 0.070 pg C μm^{-3} is similar to the average value of 0.089 ± 0.055 pg C μm^{-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, on bacteria). In addition, CHN data on the (benthic) foraminifer *Ammonia tepida* indicate that foraminifer protein-biomass equals carbon-biomass (Movellan, 2012).

Smaller planktic foraminifer specimens have much higher average conversion factors of 0.413 ± 0.040 pg C μm^{-3} (at 100 μm 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 stock and biomass production

The majority of planktic foraminifers is living in the surface oceans, hemipelagic oeans, 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 and associated deep chlorophyll maximum (DCM). Accordingly, the 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

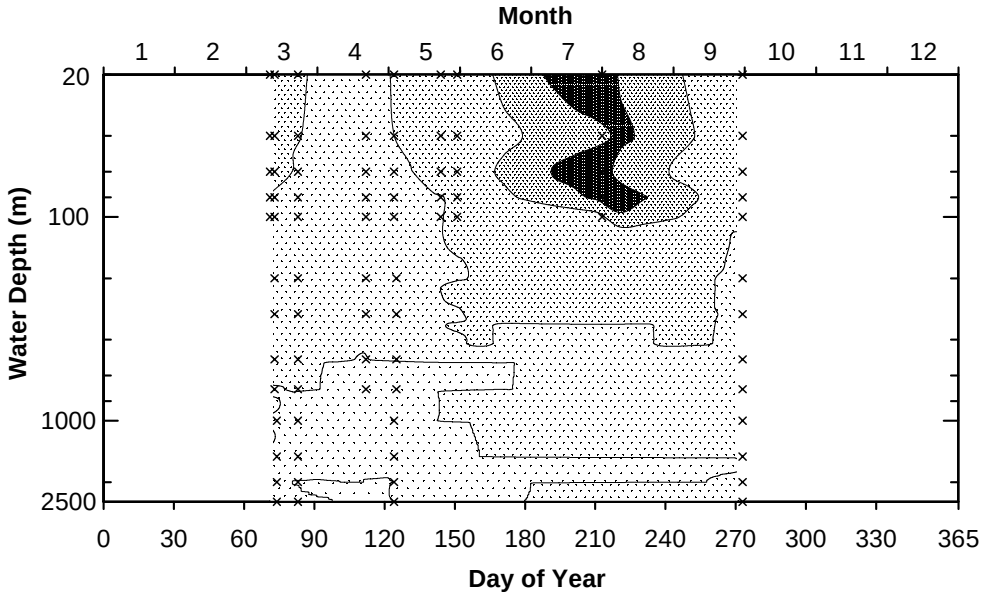

Figure 11. Average temporal development of planktic foraminifer assemblage > 125 μm protein-biomass at WAST, Arabian Sea at 20° N, 60° E. $n = 80$ data points (0–2500 m water depth) in 1995 and 1997 (Table 1). Water depths refer to the lower limits of the sampled water depth intervals. Gray levels correspond to > 200, > 100–200, > 10–100, > 1–10, > 0–1, and 0 μg C m^{-3}. White = time interval not sampled. Resolution: $z = 20$ m water depth, $t = 10$ days, using quadrant interpolation.

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 foraminiferal 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 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 1989 and 1999 (Fig. 2), the average PFAB > 125 μm test-size sums up to a global average of 2.93–11.27 mg C m^{-2} (geometric mean and arithmetic mean, respectively) at any point of time (Table 4: 2934.11–11265.13 μg 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 ocean is taken as 290×10^6 km^2 (Milliman and Droxler, 1996; total area = 362.03×10^6 km^2, cf. Dietrich et al., 1975). This excludes areas of the global ocean, in which planktic foraminifer reproduction, and hence 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 290×10^6 km^2 inhabited by fully developed planktic foraminifer faunas might be a rather conservative guess, though, since Retailleau et al. (2009, 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 32×10^6 km^2 to 322×10^6 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 per year on average, the global planktic foraminifer biomass production (> 125 μm) amounts to 8.5–32.7 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 μm, though, excluding smaller

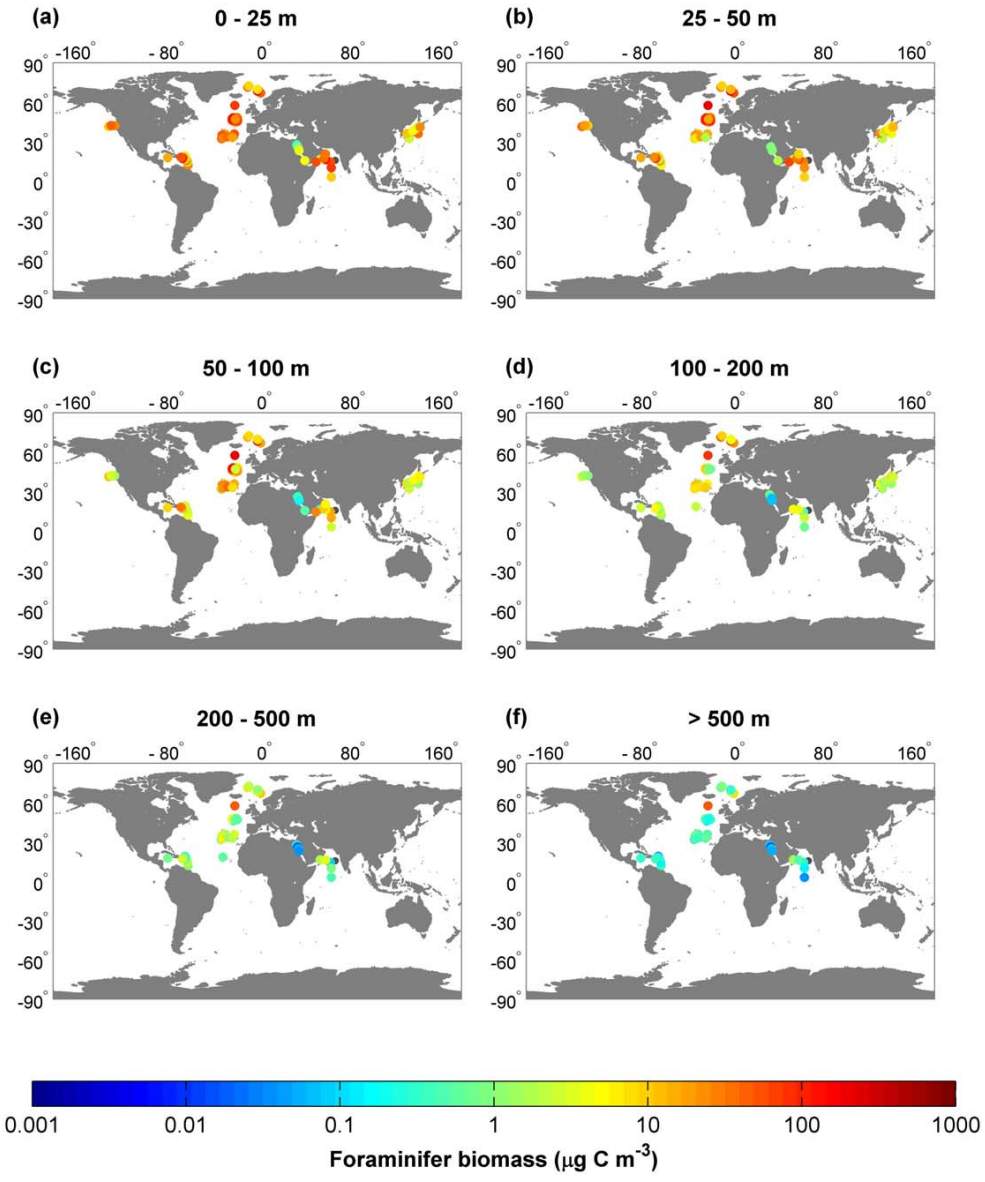

Figure 12. Log-normalised average depth related PFAB (Log_{10} µg C m^{-3}) binned on a 3 × 3° grid, comprising the North Atlantic Ocean, Caribbean, Arabian Sea and Gulf of Aden, and Red Sea.

individuals of ~ 12–125 µm in size (cf. Brummer and Kroon, 1988). Given that the number of individuals of a population decreases over time, and assuming that the average faunal contribution of individuals > 100–125 µm in size amounts to 50 % of the total fauna > 100 µm (Table 3; Schiebel and Hemleben, 2000), the numbers given above (> 125 µm) would possibly be twice as high when including individuals > 100–125 µm, and more than three time 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 ~ 25–100 Tg C yr^{-1}, which is about half that of the estimated diazotroph biomass (Luo et al., 2012: 40–200 Tg C), and ~ 3–5 % the biomass of diatoms (Leblanc et al., 2012: ~ 500–3000 Tg C).

4.2 Uncertainties of the PFAB estimates

This paper presents a first estimate of regional 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 to improve spatial coverage. 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 PFAB estimate. In addition, we will try to include data on biomass and standing

stocks of small (including juvenile and neanic) specimens, as well as 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. Finally, intercomparison of planktic foraminifer biomass data from laboratories using different methods of biomass analyses would be needed to verify the data presented here to enlarge the so far rather limited data set. Considering all of the uncertainties, the numbers given above need to be used with care, but seem to be reasonable in comparison to the estimates of other groups of plankton, for example, diazotrophs and diatoms presented by Luo et al. (2012) and Leblanc et al. (2012).

5 Conclusions

The protein biomass analysed with the bicinchoninic acid (BCA) method 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 $>125\,\mu m$ in test size for a total of 1128 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 $322 \times 10^6\,km^2$, which supports planktic foraminifer production over nine month per year results in a global planktic foraminifer biomass of ~ 8.5–$32.7\,Tg\,C\,yr^{-1}$. Including juvenile and neanic planktic foraminifers $<125\,\mu m$ in test size the total planktic foraminifer biomass production is assumed at ~ 25–$100\,Tg\,C\,yr^{-1}$.

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