

Planktic foraminiferal dissolution in the twilight zone

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Abstract

Calcite dissolution of planktic foraminifers that settle from the surface ocean to depths has been assessed using the weight/size relationship of tests and correlated to carbonate ion concentration ($[\text{CO}_3^{2-}]$) of ambient sea water. *Globigerina bulloides* and *Globigerinita glutinata* were sampled from the North Atlantic and the Arabian Sea during different seasons (spring and fall and the monsoons, respectively). Test weight has been determined for single tests from narrow size classes ($250 \pm 8 \mu\text{m}$ and $300 \pm 7 \mu\text{m}$ minimum test diameter). Initial test weight of both species in surface waters differs between regions and seasons. Weight loss of settling tests in the twilight zone between 100 and 1000 m water depths averaged 19%. Below the twilight zone (1000–2500 m) no weight loss occurs on average, and tests may even gain weight. Remineralization of settling planktic foraminiferal tests is most pronounced at maximum ΔCO_3^{2-} . Accordingly, strong dissolution occurs in the twilight zone, at the depth of maximum decrease in ΔCO_3^{2-} . It is assumed that dissolution of planktic foraminiferal calcite is caused by CO_3^{2-} (under-) saturation inside the test, buffered by diffusive exchange of CO_3^{2-} ions with the ambient sea water through the pores and aperture. Consequently, reconstruction of small-scale differences in seawater $[\text{CO}_3^{2-}]$ from test weight alone is not feasible and systematic correlation between test weight and ΔCO_3^{2-} of the ambient sea water is statistically not significant. At constant $[\text{CO}_3^{2-}]$, remineralization cannot be deduced from test weight, neither at high nor low CO_3^{2-} saturation. In total, our data suggest that the global vertical planktic foraminiferal CaCO_3 flux is about 19% lower than calculated by Schiebel [2002. Planktic foraminiferal sedimentation and the marine calcite budget. *Global Biogeochemical Cycles*, 16 (4), 1065 [doi: 10.1029/2001GB001459]].

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1. Introduction

Planktic foraminifers are major producers of marine particulate calcite and calcareous sediments in modern oceans. Calcareous plankton effectively mediate the global carbon turnover because of their short response times and feedbacks on changes in atmospheric and terrestrial carbon exchange (Zeebe

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and Westbroek, 2003). The formation, flux and sedimentation of biogenic carbonate define the so-called inorganic pump, which effectively lowers carbonate saturation and increases $p\text{CO}_2$ of surface waters. Furthermore, planktic foraminiferal tests have been used to reconstruct the carbonate ion concentration ($[\text{CO}_3^{2-}]$) of the deep sea (e.g., Broecker and Clark, 2001, 2002). These papers acknowledge that dissolution in marine sediments is a function both of bottom and pore water $[\text{CO}_3^{2-}]$ and that initial test weights may not be constant. In fact, it has been shown that initial test weights are not constant, and are possibly controlled by $[\text{CO}_3^{2-}]$ (Barker and Elderfield, 2002; Bijma et al., 1999, 2002). It also has been demonstrated that variations in the delivery of organic matter may cause significant offsets in the saturation state between bottom-waters and sediment pore waters (Schulte and Bard, 2003; de Villiers, 2005).

Secondary calcification, selective dissolution, and weight change of planktic foraminiferal tests have been modeled on the basis of observations on tests of *Globorotalia truncatulinoides* and *Globigerinoides sacculifer* by Lohmann (1995). In order to complete and to calibrate the planktic foraminiferal CaCO_3 inventory, the prerequisites that determine whether dissolution or encrustation take place would need to be known. Seawater $[\text{CO}_3^{2-}]$ has been discussed as the obvious cause of test calcite precipitation/dissolution (e.g., Broecker and Clark, 1999). However, $[\text{CO}_3^{2-}]$ and remineralization of tests in the water column are not well correlated, and dissolution within ‘microenvironments’ has been proposed (Schiebel et al., 1997b; Milliman et al., 1999). Such microenvironments are not well understood. While the effect of $[\text{CO}_3^{2-}]$ on foraminiferal shell production and hence weight has been assessed by laboratory experiments (Bijma et al., 1999), experiments on shell dissolution within the water column have not yet produced convincing results (Dittert et al., 1999). The large range in the spatial and temporal scale of biogeochemical effects that act on foraminiferal tests (e.g., differential settling velocity over great water depths) in the ocean cannot be verified in the laboratory. In summary, the dissolution of tests is not yet sufficiently understood (cf. Schiebel, 2002), and needs to be assessed by analyzing planktic foraminiferal tests from the water column, along with *in situ* biogeochemical data, in order to understand remineralization and facilitate reconstruction of past $[\text{CO}_3^{2-}]$ from planktic foraminiferal test weight.

In this study we aim towards a mechanistic understanding of the dissolution of planktic foraminiferal tests with different dissolution susceptibilities (Dittert et al., 1999) by analyzing samples from two regions that span a wide range in hydrographic properties including $[\text{CO}_3^{2-}]$ (i.e. the North Atlantic and Arabian Sea) (Broecker and Peng, 1982). This will allow the application of our findings to other modern planktic foraminiferal species in a wide range of oceanographic settings. The main objective of this study is (a) to disentangle planktic foraminiferal test flux and CaCO_3 dissolution across the twilight zone, (b) to assess the relationship between test weight and $[\text{CO}_3^{2-}]$ in the water column, (c) to quantify calcite dissolution of settling tests, and (d) to refine the assessment of the global planktic foraminiferal CaCO_3 flux budget.

2. Methods and material

2.1. Sampling techniques and material

Size normalized test weights (250 and 300 μm) of individual planktic foraminiferal tests were measured for two species collected from the water column using vertical multinet hauls (Schiebel et al., 1995). *Globigerina bulloides* and *Globigerinita glutinata* were sampled in the eastern North Atlantic (47°N, 20°W) and Arabian Sea (16°N, 60°E) between the sea surface and 2500 m water depth (Table 1). Both species are ubiquitous surface dwellers with minor variation in test morphology and are barren of symbionts (Hemleben et al., 1989). Both species are well known for their life cycles and ecology (Schiebel et al., 2001; Schiebel and Hemleben, 2005). Virtually all specimens >150 μm in diameter have undergone gametogenesis (Schiebel et al., 1997a,b). Accordingly, both species are ideally suited for comparison on global scale.

2.2. Cytoplasm weight and absolute test weight

Tests containing remnants of dry cytoplasm versus empty tests were recorded. Cytoplasm in dry tests is visible as a small pigmented patch (mostly green or red) at the inside of the last or second to last chamber. The presence or absence of cytoplasm within the settling foraminiferal test has no statistically significant effect on the change of test weight (Fig. 1). Following Altenbach (1985), a

Table 1

Sampling details of planktic foraminiferal tests and geochemical measurements to determine $[\text{CO}_3^{2-}]$

Cruise	Station	Day	Year	Lat.	Long.	Water depth (m)	Gear	Sampling depth (m)
M21/1	96	April 1	1992	47°15.92'N	19°31.01'W	4560	MN	0–100
	96	April 1	1992	47°15.92'N	19°30.96'W	4559	CTD	10–98
	99	April 2	1992	47°17.77'N	19°30.64'W	4541	MN	100–700
	99	April 2	1992	47°17.26'N	19°30.84'W	4542	CTD	101–498
	99	April 2	1992	47°17.29'N	19°30.88'W	4542	MN	700–2500
	103	April 3	1992	47°05.09'N	19°24.28'W	4380	CTD	696–2496
M36/5	354	Sept. 30	1996	48°35.71'N	22°23.05'W	4142	MN	0–100
	354	Sept. 30	1996	48°35.75'N	22°23.23'W	4133	MN	100–700
	354	Sept. 30	1996	48°35.82'N	22°22.72'W	4150	MN	700–2500
NOAA	66	Aug. 23	1993	48°00.00'N	20°00.02'W	—	CTD	0.5–4381.1
M33/1	601	Sept. 30	1995	16°09.20'N	60°25.69'E	4029	MN	0–100
	601	Sept. 30	1995	16°08.99'N	60°25.86'E	4028	MN	100–700
	601	Sept. 30	1995	16°08.98'N	60°25.82'E	4028	MN	700–2500
SO120	032-1 to 23	July 2	1997	16°47.40'N	60°30.00'E	4021	CTD	17–4006

Foraminifers were sampled with a multinet (MN), and water chemistry was conveyed on water samples with a CTD/rosette. Carbonate data of August 1993 are available from the NOAA/OACES/CO2 web page.

wet weight of cytoplasm equal to 10% of the test weight is assumed. At a given density of cytoplasm of 1.027 g cm^{-3} (Saidova, 1967), the dry weight of cytoplasm is 0.26% of the test weight, which is two orders of magnitude lower than the total test weight change and hence assumed negligible (cf. Fig. 2).

2.3. Test morphometry

Tests from a narrow size range were picked from pre-sieved size fractions $>200\text{--}250 \mu\text{m}$ and $>250\text{--}315 \mu\text{m}$. Selection of morphologically similar test and morphometric analysis was carried out with an automated incident light microscope (AFLA) using AnalySIS software (Bollmann et al., 2004). According to the test size measured by ALFA (minimum, maximum and average test length; surface area of test in umbilical view), 5–24 tests were selected for weighing. Tests were carefully selected from a narrow size fraction because an increase in the length of a test may lead to a corresponding increase in weight, larger by a power of $\sim 1.5\text{--}2.5$, depending on the size–volume relationship (Schiebel and Hemleben, 2000; Barker and Elderfield, 2002). The average range of test size (minimum diameter) of the selected specimens was $250 \pm 8 \mu\text{m}$ and $300 \pm 7 \mu\text{m}$. Test size was normalized (D_{NORM}) according to the minimum test diameter for the smaller and larger tests to $D = 250$ and $300 \mu\text{m}$, respectively.

2.4. Determination of test weight

The tests were weighed using a seven-place Mettler-Toledo microbalance (precision of $0.1 \mu\text{g}$). In general, 20 tests from the smaller size fraction ($250 \mu\text{m}$), and 10 tests of the larger size fraction ($300 \mu\text{m}$) were weighed. Tests of each size fraction were weighed together to improve reproducibility of weighing results. The weight of the test assemblage was then divided by the number of tests weighed to give the mean weight for the population (Tables 2–4).

The minimum test diameter (D_{TEST}) and the average measured test weight (W_{SIZE}) of each species were used to normalize the mean weight (W_{NORM}) of the sample to the average size for both $D_{\text{NORM}} = 250$ and $300 \mu\text{m}$ fractions using the following equation:

$$W_{\text{NORM}} = (W_{\text{SIZE}}/D_{\text{TEST}}) * D_{\text{NORM}}. \quad (1)$$

Applying Eq. (1), we assume that test weight increases linearly with test diameter, which is possibly not the case, but which is of negligible relevance taking into account the limited variability of the test diameter ($D = 15.1 \pm 0.9 \mu\text{m}$) within a sample. All further discussion is based on the normalized test weight W_{NORM} .

2.5. Carbonate system data

Carbonate system data for the North Atlantic (M21/1 and M36/5) are calculated from total

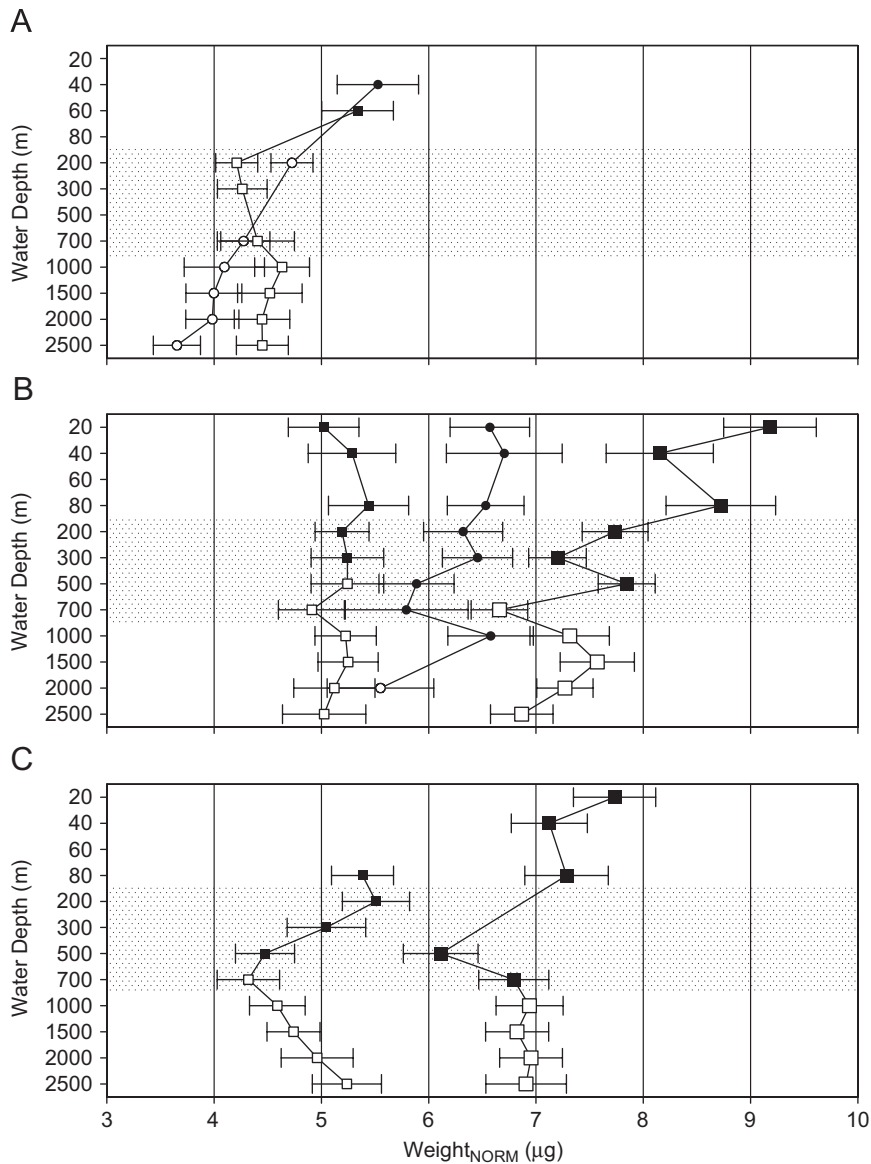


Fig. 1. Normalized weight versus water depth (A) in the North Atlantic during spring (cruise M21/1), (B) in the North Atlantic during autumn (cruise M36/5) and (C) in the Arabian Sea during SW monsoon (cruise M33/1). Standard deviation is given as error bars. Tests with cytoplasm are indicated by filled symbols, empty tests by open symbols. Large squares represent large *G. bulloides* ($D_{\text{NORM}} = 300 \mu\text{m}$), small squares represent small *G. bulloides*, and circles represent small *G. glutinata* ($D_{\text{NORM}} = 250 \mu\text{m}$). Shading indicates the twilight zone. Note that the depth scale is not linear.

alkalinity (TA) and total dissolved inorganic carbon (TC) measured by potentiometric titration (Pegler and Kempe, 1993). Data from NOAA (Table 1) are available from the web site (http://cdiac.esd.ornl.gov/oceans/woce_a16n.html). In order to account for the degree of deviation in calculating $[\text{CO}_3^{2-}]$, we allowed an uncertainty of

1% for the TC data of M21/1 (Table 2). $[\text{CO}_3^{2-}]$ of the Arabian Sea was calculated from TA measured by potentiometric titration, and DIC measured by coulometric titration (Lendt et al., 2003). Carbonate data and calcite saturation level (Ω) have been calculated after Lewis and Wallace (1998) using the refit of the equilibrium constants by Mehrbach et al.

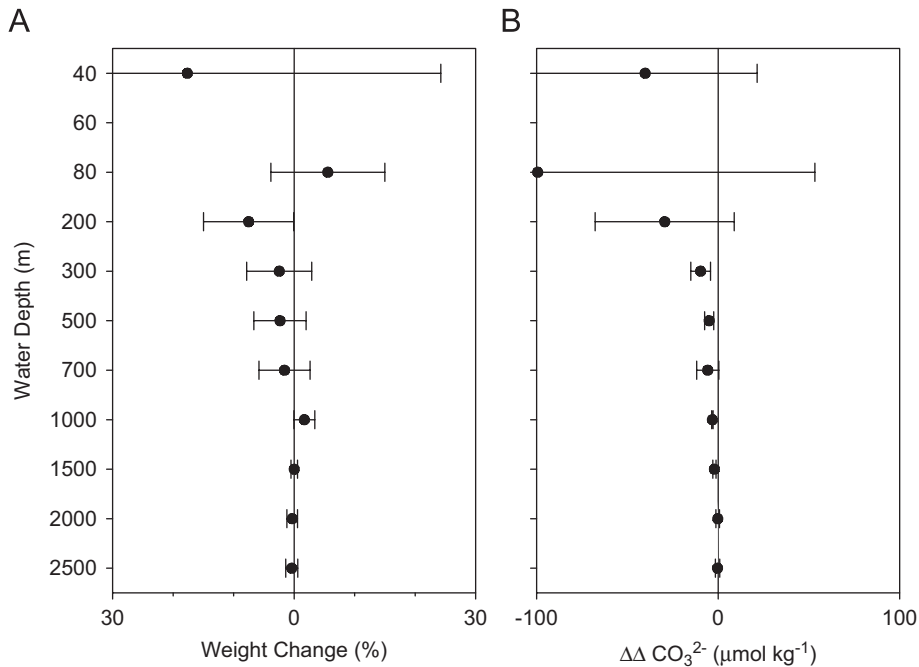


Fig. 2. (A) Average relative change of normalized test weight (Tables 2–4). Relative changes in weight refer to the nearest sample above; i.e. at 40 m tests are about 18% lighter than at 20 m water depth. Weight change is normalized to 100-m depth increment. Changes in the North Atlantic (Tables 2 and 3) and in the Arabian Sea (Table 4) are within the standard deviation of the average weight change. (B) Difference of ΔCO_3^{2-} normalized to 100-m depth increment. Differences in ΔCO_3^{2-} in surface waters between oceans and seasons cause the huge standard deviation (error bars). Note that the depth scale is not linear.

Table 2

Normalized weight of tests of *G. bulloides* and *G. glutinata* collected during Meteor cruise 21/1

Water depth (m)	<i>G. bulloides</i> (μg)	D_{250} (σ)	<i>G. bulloides</i> (μg)	D_{300} (σ)	<i>G. glutinata</i> (μg)	D_{250} (σ)	Water depth* (m)	$[\text{CO}_3^{2-}]$ calc.	$[\text{CO}_3^{2-}]$ +1% DIC	$[\text{CO}_3^{2-}]$ -1% DIC	Ω (Calcite)	ΔCO_3^{2-}
10	—	—	—	—	—	—	10	156.7	143.9	169.8	3.72	114.80
20	5.02	0.33	9.18	0.43	6.57	0.37	20	155.9	143.1	169.0	3.70	113.93
34	—	—	—	—	—	—	34	154.8	142.0	167.8	3.66	112.72
40	5.28	0.41	8.15	0.50	6.70	0.54	40	155.3	142.5	168.3	3.67	113.18
53	—	—	—	—	—	—	53	156.4	143.5	169.4	3.69	114.16
80	5.44	0.37	8.72	0.51	6.53	0.36	80	158.1	145.2	171.1	3.71	115.70
200	5.19	0.25	7.74	0.31	6.32	0.37	201	154.5	141.7	167.6	3.55	111.27
300	5.24	0.34	7.20	0.27	6.45	0.33	300	142.1	129.3	155.0	3.21	98.18
500	5.24	0.34	7.85	0.27	5.89	0.35	498	136.0	123.3	148.9	2.96	91.08
700	4.91	0.31	6.66	0.26	5.79	0.58	696	117.2	105.0	129.8	2.47	90.52
1000	5.22	0.29	7.31	0.37	6.58	0.40	994	109.8	97.8	122.2	2.17	66.66
1500	5.25	0.28	7.57	0.35	—	—	1489	100.5	88.9	112.6	1.80	45.02
2000	5.12	0.38	7.27	0.26	5.55	0.50	1985	108.8	96.9	121.0	1.76	47.33
2500	5.02	0.39	6.87	0.29	—	—	2496	110.7	98.8	122.9	1.62	42.71

Water depth (m) is the lower level of the multinet sampling interval. Water depth* (m) gives a discrete depth of CO_3^{2-} concentration calculated with the measured DIC, and with +1% DIC and -1% DIC to account for possible deviation of data. Interpolated data are given in italics. σ = standard deviation.

(1973) according to Dickson and Millero (1987, 1989). Carbonate concentration is normalized for the calcite saturation level (Ω) using Eq. (2) (cf.

Broecker and Clark, 1999)

$$\Delta[\text{CO}_3^{2-}] = [\text{CO}_3^{2-}] - ([\text{CO}_3^{2-}]/\Omega). \quad (2)$$

Table 3
Normalized weight of tests of *G. bulloides* collected during Meteor cruise 36/5

Water depth (m)	<i>G. bulloides</i> (μg)	<i>D</i> ₂₅₀ (σ)	<i>G. bulloides</i> (μg)	<i>D</i> ₃₀₀ (σ)	Water depth* (m)	[CO ₃ ²⁻] calc.	Ω (Calcite)	Δ CO ₃ ²⁻
20	—	—	7.73	0.38	19	216.1	5.12	173.89
40	—	—	7.12	0.35	42	190.7	4.49	148.23
68	—	—	—	—	68	169.9	3.98	127.21
80	5.38	0.29	7.29	0.39	80	166.5	3.89	123.69
98	—	—	—	—	98	161.3	3.76	118.40
200	5.51	0.31	—	—	201	151.3	3.46	107.57
300	5.05	0.37	—	—	298	148.7	3.34	104.18
397	—	—	—	—	397	142.5	3.15	97.26
500	4.47	0.28	6.11	0.35	500	134.3	2.91	88.07
542	—	—	—	—	542	130.9	2.81	84.32
700	4.32	0.29	6.79	0.33	691	119.9	2.50	71.94
1000	4.59	0.26	6.94	0.31	989	114.5	2.25	63.61
1500	4.74	0.25	6.82	0.29	1481	110.1	1.95	53.64
2000	4.96	0.34	6.95	0.29	1975	109.3	1.75	46.84
2500	5.24	0.32	6.91	0.38	2466	110.3	1.60	41.36

Interpolated data are given in italics. σ = Standard deviation. For further explanation see Table 1.

Table 4
Normalized weight of tests of *G. bulloides* and *G. glutinata* collected during Meteor cruise 33/1

Water depth (m)	<i>G. bulloides</i> (μg)	<i>D</i> ₂₅₀ (σ)	<i>G. glutinata</i> (μg)	<i>D</i> ₂₅₀ (σ)	Water depth* (m)	[CO ₃ ²⁻] calc.	Ω (Calcite)	Δ CO ₃ ²⁻
40	—	—	5.53	0.38	37	253.4	6.04	211.4464
60	5.34	0.33	—	—	57	253.2	6.02	211.1402
200	4.21	0.20	4.72	0.20	207	85.0	1.95	41.41026
300	4.26	0.23	—	—	308	73.3	1.65	28.87576
700	4.40	0.34	4.27	0.25	699	72.6	1.52	24.83684
1000	4.63	0.26	4.09	0.37	1004	66.0	1.30	15.23077
1500	4.52	0.30	4.00	0.26	1517	65.1	1.16	8.97931
2000	4.45	0.26	3.98	0.25	2009	72.7	1.16	10.02759
2500	4.45	0.24	3.65	0.22	2522	84.7	1.22	15.27377

Interpolated data are given in italics. σ = Standard deviation. For further explanation see Table 1.

Calcite supersaturation is given for Ω > 1, and values of Ω < 1 define undersaturated waters.

3. Results

3.1. Test weight change with water depth

Test weights of both *G. bulloides* and *G. glutinata* from both size classes 250 μm and 300 μm decrease between the surface ocean and the deep twilight zone at 700–1000 m water depth (Fig. 1, Table 1). Weight losses for *G. bulloides* and *G. glutinata* do not differ significantly. Average test weights increase from the intermediate mixed layer towards the pycnocline, from 40 to 80 m depth, respectively (Fig. 2A). Species-specific test weights in the mixed layer vary considerably (Fig. 2A). Within the

twilight zone at 100–700 m depth, test weights decrease significantly (19.4%) and below increase on average by ~1%. The total average weight loss of planktic foraminiferal tests analyzed between 40 and 2500 m water depth is about 19%.

In the North Atlantic (M21/1 and M36/5), cytoplasm is found in tests above 1000 m water depth. In the Arabian Sea, cytoplasm-bearing tests were found only above 100 m water depth. In both areas test weight generally decreases within the twilight zone, independent of the presence of cytoplasm within the tests (Fig. 1). The absolute weight loss appears to be independent of test size although large tests (300 μm) occasionally lose more weight than small test (250 μm) of the same species (*G. bulloides*) from within the same samples (Fig. 1; M21/1).

3.2. Test weight change with ΔCO_3^{2-}

At the studied sites, ΔCO_3^{2-} generally decreases with depth and all sampling depths are supersaturated with respect to calcite (Figs. 2B and 3; Tables 2–4; $\Omega > 1$). Maximum variability of ΔCO_3^{2-} occurs in the surface mixed layer of the ocean, and the maximum decrease in ΔCO_3^{2-} occurs across the pycnocline. In the twilight zone, ΔCO_3^{2-} decreases significantly, and below 1000 m depth ΔCO_3^{2-} occasionally increases by a small amount (Fig. 2B). In the Arabian Sea, ΔCO_3^{2-} increases below the twilight zone between 1500 and 2500 m, from 9 to $15 \mu\text{mol kg}^{-1}$.

G. bulloides and *G. glutinata* from the Arabian Sea are lighter on average than those from the North Atlantic, despite higher $[\text{CO}_3^{2-}]$ of Arabian Sea surface waters (Figs. 2 and 3). Planktic foraminiferal test weights generally decrease as tests settle from surface waters through the twilight zone, across a wide range of ΔCO_3^{2-} (~ 10 – $220 \mu\text{mol kg}^{-1}$) (Fig. 4). Below the twilight zone, ΔCO_3^{2-} occasionally increases slightly (Fig. 3), and

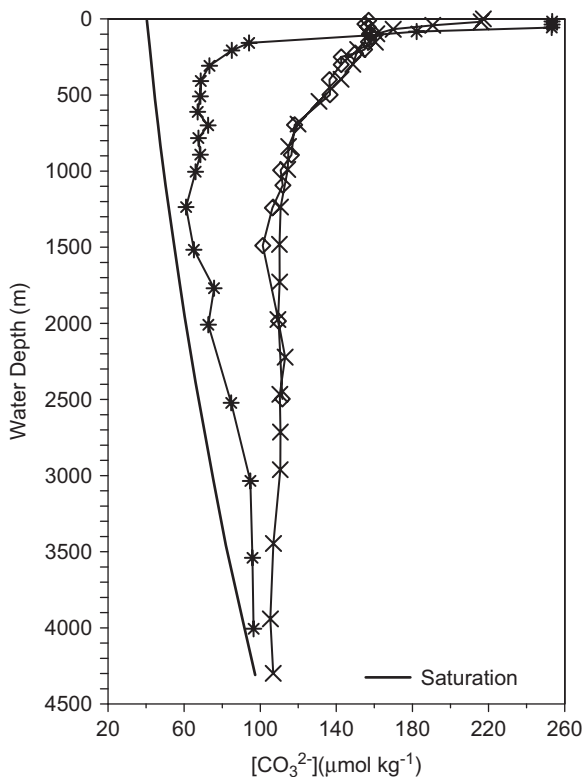


Fig. 3. $[\text{CO}_3^{2-}]$ in the North Atlantic during spring (diamonds) and fall (crosses), and in the Arabian Sea during SW monsoon (asterisks). Calcite saturation data are given in Tables 2–4.

test weights of single specimens occasionally increase, independent of test size and species (Figs. 1 and 4). Although a general trend of test weight loss with decreasing ΔCO_3^{2-} and weight gain with increasing ΔCO_3^{2-} is evident, the correlation of changing ΔCO_3^{2-} and test weight is statistically not significant and error probability is high (Fig. 4A and B). More significant correlation of changes in test weight and $\Delta[\text{CO}_3^{2-}]$ in the Arabian Sea (Fig. 4C) is due to the larger changes in these parameters.

4. Discussion

Planktic foraminiferal test weight has been applied as a proxy for bottom water $[\text{CO}_3^{2-}]$ (e.g., Broecker and Clark, 2001). The reconstruction presented by Broecker and Clark (2002) relied on the assumption that planktic foraminiferal tests of a given size range are rather uniform and are not influenced by dissolution until they arrive at the ocean floor. That this is not the case has been shown by, for example, Milliman (1974), Milliman et al. (1999) and Schiebel (2002, and references therein). Bijma et al. (2002) discuss the dependence of initial planktic foraminiferal test weight on growth conditions (e.g., $[\text{CO}_3^{2-}]$ and temperature, light (in case of symbiont-bearing species)). Tests with high-dissolution susceptibility have been shown to dissolve even in supersaturated waters (above the lysocline), which is above ~ 4500 m water depth in the North Atlantic (see Dittert et al., 1999, for a compilation of data; cf. Schulte and Bard, 2003). In the case where dissolution is not complete, i.e. tests are not entirely dissolved, partial dissolution would affect the weight of tests. Vice versa, calcite crusts might be added, test walls increase in thickness and test gain weight (Lohmann, 1995; Simstich et al., 2003). A summary of the factors that affect planktic foraminiferal test weight is given by Schiebel and Hemleben (2005).

4.1. Initial test weight

Although surface water temperature and $[\text{CO}_3^{2-}]$ in the Arabian Sea are significantly higher than in the North Atlantic (Fig. 3), initial (growth) test weight is similar or even lower than in the North Atlantic. Under thermodynamic consideration alone, the opposite should be the case, and therefore other effects are probably involved. Differences in environmental factors such as nutrient availability, and to what degree the ecologic conditions are

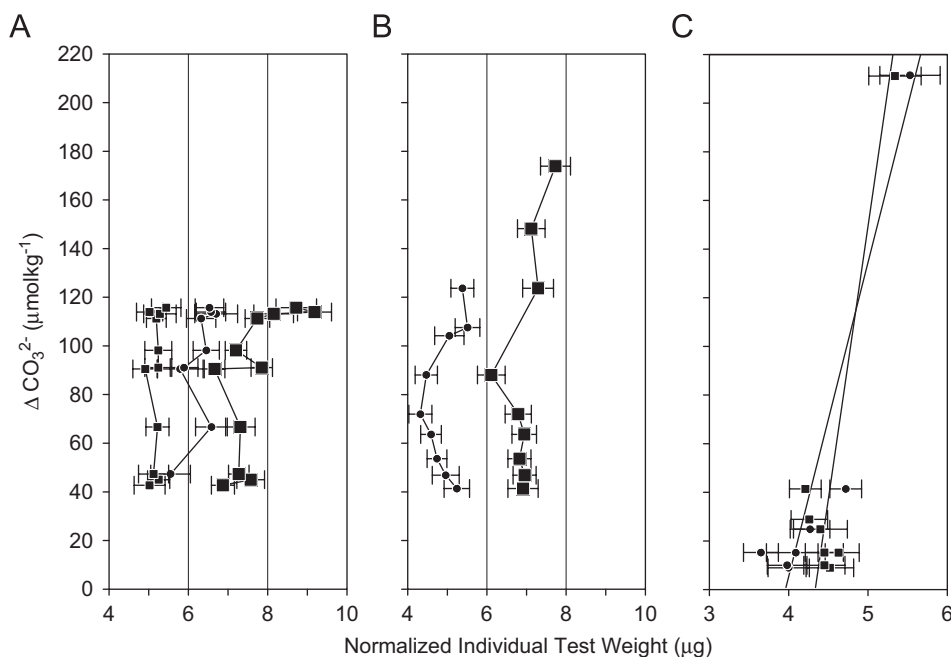


Fig. 4. Individual planktic foraminiferal test weight and ΔCO_3^{2-} (A) in the North Atlantic during spring (M21/1), (B) in the North Atlantic during autumn (M36/5) and (C) in the Arabian Sea during SW monsoon (M33/1). Although trends in test weight versus ΔCO_3^{2-} data in the North Atlantic (panels A and B) were observed, no statistically significant correlation does exist. In the Arabian Sea (panel C), test weights of *G. bulloides* (squares) and *G. glutinata* (dots) are correlated to ΔCO_3^{2-} with $r^2 = 0.74$ ($n = 8$, $p < 0.01$) and $r^2 = 0.83$ ($n = 7$, $p < 0.01$), respectively. Symbols are the same as in Fig. 1.

favorable for the production of the shell for different species, are under investigation but not yet fully understood. In addition to ecological (Schiebel and Hemleben, 2005), evolutionary (Schmidt et al., 2004) and chemical effects (Bijma et al., 1999; Barker and Elderfield, 2002), differences in initial test weights between the Atlantic Ocean and Arabian Sea could result from the presence of different genotypes of similar morphospecies (Darling et al., 2000), which are not distinguishable by incident light microscopy. However, since specimens of both species used in this study have been picked from samples that include a sufficient number of individuals, these samples should represent favorable growth conditions of both species. Symbiotic activity, as a cause of weight difference, can be excluded because both species are symbiont barren (Erez, 1983; Hemleben et al., 1989). However, lower initial test weight might explain the low weight of tests at surface sediments of the Indian Ocean, which are lower than for Atlantic and Pacific sediments for similar values of $\Delta[\text{CO}_3^{2-}]$ (Broecker and Clark, 2001).

4.2. The effect of exposure time on weight loss

Broecker and Clark (2001) describe a weight loss of $0.3 \mu\text{g} \mu\text{mol CO}_3^{2-} \text{ kg}^{-1}$ for planktic foraminiferal tests sampled from sediment cores. In our study, test weight loss does not significantly correlate with ΔCO_3^{2-} change. The different response of test weight to ΔCO_3^{2-} change must be dependent on the absolute value of ΔCO_3^{2-} , but also possibly relates to the nature of the samples analyzed: Broecker and Clark (2001) analyzed specimens from sediments and we analyzed tests from the water column. In surface sediments, tests are exposed to bottom waters for a considerably longer time (months to thousands of years) than tests which are sinking through the water column (several days to weeks) (Schiebel and Hemleben, 2000, and references therein). As the amount of dissolution depends both on ΔCO_3^{2-} and exposure time, the difference between our findings and the results of Broecker and Clark (2001) might be partly explained by the exposure time. Additionally, it is likely that the generally lower saturation state

($\Delta[\text{CO}_3^{2-}] < 20 \mu\text{mol kg}^{-1}$) of waters bathing the sites employed by Broecker and Clark (2001) would induce higher rates of dissolution.

4.3. Seasonality of initial test weight and deep-water test weight

Tests of *G. bulloides* (300 μm) sampled from the surface North Atlantic in spring are significantly heavier than in fall (Fig. 1). Smaller tests (250 μm , at 80 m depth) have the same weight in spring and fall. Since ambient surface ocean $[\text{CO}_3^{2-}]$ is higher in autumn, the results suggest that shell weight is probably controlled by other factors in addition to $[\text{CO}_3^{2-}]$. Mass production of *G. bulloides* in the North Atlantic occurs during spring, which is possibly the season most ecologically favorable for this species (Schiebel and Hemleben, 2000). The sum of the ecologic conditions is obviously more important than single parameters, and we cannot quantify which ecologic parameter determines the weight of tests. At 2500 m water depth, during both spring and fall, *G. bulloides* tests (250 and 300 μm) are similar in weight. Consequently, certain variations in initial weight may not be reflected deeper in the water column or at the sea floor.

4.4. Pulsed flux and the comparability of different water depths

Planktic foraminiferal test assemblages at different water depths are not directly comparable with each other. Test flux is pulsed according to reproduction and growth of specimens (Bijma et al., 1994; Schiebel et al., 1995). Allowing for species- and size-specific settling velocities, tests at deeper waters were probably produced and exported from the productive layer earlier than tests from shallower waters. The difference in export time of specimens from adjacent water depth intervals is possibly several hours to some days (Schiebel and Hemleben, 2000). Taking into consideration that the average life span of adult specimens of both species *G. bulloides* and *G. glutinata* is about one month (Schiebel et al., 1997a,b; Schiebel and Hemleben, 2005), and that test weight and chemical composition represent an integration over the entire time of test production, we assume tests from adjacent water depths are similar in chemical composition and test weight.

4.5. Dissolution of tests in the water column

The weight of planktic foraminiferal test is possibly determined by growth conditions in the productive zone (Hemleben et al., 1989). Ontogenetic weight gain and encrustation of *G. bulloides* and *G. glutinata* do occur in the life habitat above the seasonal pycnocline (Schiebel and Hemleben, 2005), but systematic subsurface encrustation is unlikely considering the general test weight loss with increasing depth (Fig. 1). Single peaks (positive and negative) in the vertical test weight distribution (Fig. 1) are possibly caused by initial differences in test weight (pulsed flux). The presence or absence of cytoplasm does not obviously affect the test weight (Fig. 1). Individual test weight loss below the pycnocline is possibly caused by calcite dissolution while tests settle through the water column (Fig. 1). Significant simultaneous decrease in ΔCO_3^{2-} and test weight in the twilight zone (Fig. 2) indicates that the remineralization of tests is affected by the change in $[\text{CO}_3^{2-}]$. Below the twilight zone at 1000–2500 m water depth, changes in test weight and ΔCO_3^{2-} are much smaller than above, although absolute ΔCO_3^{2-} is much lower (Fig. 3). This indicates that remineralization of planktic foraminiferal test calcite coincides with gradients in ΔCO_3^{2-} at 100–700 m depth, in waters which are supersaturated with regard to calcite (Figs. 2B and 3).

Because waters in the twilight zone of the studied areas are supersaturated with respect to calcite, dissolution must occur within an undersaturated micro-environment within the test itself. The saturation state of waters inside the test might be lowered by remineralization of organic matter and bacterial activity. Exchange of waters between the inside and the outside of tests is unlikely because the flow of waters at outer test walls is rather laminar than turbulent (Fok-Pun and Komar, 1983). Gradients in $[\text{CO}_3^{2-}]$ between the outside and inside of tests would therefore need to be balanced by diffusion, and changes in $[\text{CO}_3^{2-}]$ of ambient sea water would then affect the inner test with a time lag that depends on the settling velocity of the test. Consequently, despite the trend between ΔCO_3^{2-} of ambient sea water and test weight observed in the North Atlantic, the correlation is probably not significant (Fig. 4A and B). In the Arabian Sea, the correlation between ΔCO_3^{2-} of ambient sea water and test weight is significant, possibly because of the gradient in ΔCO_3^{2-} , which is much steeper than in the North Atlantic (Fig. 4C).

Depending on the global applicability of the results presented here, sedimentation of planktic foraminiferal test CaCO_3 is probably much lower than previously assumed. On a global average, about 25% of the test calcite produced in surface waters has been assumed to arrive at the sea floor (Schiebel, 2002: 0.87 Gt yr^{-1}). Considering a 19% loss in calcite mass of individual tests within the twilight zone, modern global planktic foraminiferal test CaCO_3 sedimentation is now estimated at 0.71 Gt yr^{-1} .

5. Conclusions

Species-specific initial (growth) planktic foraminiferal test weight varies between ocean basins and between seasons. Seasonal differences in test weight may be obscured by dissolution in the water column, but regional differences are significant. Individual planktic foraminiferal tests in general lose about one-fifth in weight (19% CaCO_3 mass) while settling through the twilight zone between about 100 and 1000 m water depth. Below the twilight zone ($>1000 \text{ m}$ water depth), however, settling tests may actually gain mass in the case of increasing CO_3^{2-} concentration. In total, planktic foraminiferal test CaCO_3 sedimentation at the sea floor is possibly $\sim 19\%$ lower at a global scale than previously assumed and is estimated at 0.71 Gt yr^{-1} .

Dissolution and weight change of planktic foraminiferal tests cannot be directly correlated to the ΔCO_3^{2-} of ambient sea water, because dissolution and precipitation of calcite possibly take place within the test. Water exchange between ambient sea water and the inside of the test is diffusive and therefore slower than in the case of turbulent water exchange. Furthermore, in addition to carbonate chemistry of the ambient sea water, dissolution is affected by exposure time, which depends on the settling velocity of tests.

To unequivocally clarify the mechanism of remineralization of foraminiferal tests and possibly other calcite (and aragonite) particles, more data are required. Future studies need to include samples from localities that are different in planktic foraminiferal population dynamics and have different physical and chemical seawater properties. Ultra-structural breakdown of foraminiferal shell would need to be analyzed by Scanning Electron Microscopy to understand dissolution of tests within the water column, similar to the analysis of sediment samples by Dittert and Henrich (2000). Design of a

laboratory experiment that realistically simulates conditions of dissolution of tests in the water column would be most desirable.

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