



The benthic foraminiferal community in a naturally CO₂-rich coastal habitat of the southwestern Baltic Sea

K. Haynert¹, J. Schönfeld¹, I. Polovodova-Asteman², and J. Thomsen³

¹GEOMAR Helmholtz Centre for Ocean Research Kiel, Wischhofstrasse 1–3, 24148 Kiel, Germany

²Department of Earth Sciences, University of Gothenburg, P.O. Box 460, 40530 Gothenburg, Sweden

³GEOMAR Helmholtz Centre for Ocean Research Kiel, Hohenbergstrasse 2, 24105 Kiel, Germany

Correspondence to: K. Haynert (khaynert@geomar.de)

Received: 30 April 2012 – Published in Biogeosciences Discuss.: 27 June 2012

Revised: 10 October 2012 – Accepted: 23 October 2012 – Published: 12 November 2012

Abstract. It is expected that the calcification of foraminifera will be negatively affected by the ongoing acidification of the oceans. Compared to the open oceans, these organisms are subjected to much more adverse carbonate system conditions in coastal and estuarine environments such as the southwestern Baltic Sea, where benthic foraminifera are abundant. This study documents the seasonal changes of carbonate chemistry and the ensuing response of the foraminiferal community with bi-monthly resolution in Flensburg Fjord. In comparison to the surface $p\text{CO}_2$, which is close to equilibrium with the atmosphere, we observed large seasonal fluctuations of $p\text{CO}_2$ in the bottom and sediment pore waters. The sediment pore water $p\text{CO}_2$ was constantly high during the entire year ranging from 1244 to 3324 μatm . Nevertheless, in contrast to the bottom water, sediment pore water was slightly supersaturated with respect to calcite as a consequence of higher alkalinity (A_T) for most of the year. Foraminiferal assemblages were dominated by two calcareous species, *Ammonia aomoriensis* and *Elphidium incertum*, and the agglutinated *Ammotium cassis*. The one-year cycle was characterised by seasonal community shifts. Our results revealed that there is no dynamic response of foraminiferal population density and diversity to elevated sediment pore water $p\text{CO}_2$. Surprisingly, the fluctuations of sediment pore water undersaturation (Ω_{calc}) co-vary with the population densities of living *Ammonia aomoriensis*. Further, we observed that most of the tests of living calcifying foraminifera were intact. Only *Ammonia aomoriensis* showed dissolution and recalcification structures on the tests, especially at undersaturated conditions. Therefore, the benthic community is subjected to high $p\text{CO}_2$ and tolerates elevated levels as long as sediment

pore water remains supersaturated. Model calculations inferred that increasing atmospheric CO₂ concentrations will finally lead to a perennial undersaturation in sediment pore waters. Whereas benthic foraminifera indeed may cope with a high sediment pore water $p\text{CO}_2$, the steady undersaturation of sediment pore waters would likely cause a significant higher mortality of the dominating *Ammonia aomoriensis*. This shift may eventually lead to changes in the benthic foraminiferal communities in Flensburg Fjord, as well as in other regions experiencing naturally undersaturated Ω_{calc} levels.

1 Introduction

The combustion of fossil fuels and deforestation has already released about 300 Gt carbon (Archer, 2005). The release of carbon leads to rising atmospheric carbon dioxide concentrations, which causes an acidification of the oceans (Zeebe and Wolf-Gladrow, 2001). By 2100, the concentration of the ocean $p\text{CO}_2$ is expected to be approximately 750 μatm (Feely et al., 2004; Raven et al., 2005) and seawater pH is going to decrease by 0.4 units (Caldeira and Wickett, 2005). The reduced saturation state and carbonate ion concentration will cause a reduction in biogenic calcification of predominant organisms like corals, coccolithophorids and foraminifera (Gattuso et al., 1998; Kleypas et al., 1999; Bijma et al., 1999; Riebesell et al., 2000). Consequently, corrosive conditions are expected to affect the formation of carbonate skeletons of calcifying organisms (Erez, 2003; Raven et al., 2005).

Already today, calcifying organisms such as foraminifera are subjected to much more adverse carbonate system conditions in coastal marine environments as compared to the open ocean (Borges and Gypens, 2010). Especially environments such as the western Baltic Sea, which are subjected to a low salinity and alkalinity, are characterised by low carbonate ion concentrations (CO₃²⁻) and consequently lower calcium carbonate saturation states (Ω_{calc}) (Thomsen et al., 2010). Furthermore, in this area seasonal stratification of water masses, respiration in deeper layers and eutrophication induce summer hypoxia in the bottom water layers. This causes high and variable $p\text{CO}_2$ and consequently low pH during the course of the year (Diaz and Rosenberg, 2008; Conley et al., 2009; Nikulina and Dullo, 2009; Thomsen et al., 2010). In such habitats, ongoing oceanic CO₂ uptake will cause a drastic increase of the prevailing $p\text{CO}_2$ levels with peaks up to 4000 μatm by the year 2100 (Melzner et al., 2012).

Many laboratory studies have shown that calcareous foraminifera exhibited lower calcification rates under simulated future scenarios of high seawater $p\text{CO}_2$ (Le Cadre et al., 2003; Kuroyanagi et al., 2009; Allison et al., 2010; Haynert et al., 2011; Fujita et al., 2011). To date, a low number of field studies reported that calcifying organisms are negatively affected by a high $p\text{CO}_2$ in natural habitats (Fabricius et al., 2011). In proximity to hydrothermal vents, where volcanic CO₂ causes a natural decline of pH, a significant decrease in abundance and species richness of calcareous foraminifera was observed between ambient pH levels of 8.09 to 8.15 and low pH-levels of 7.08 and 7.79 close to the vents (Cigliano et al., 2010).

Calcareous benthic foraminifera are common in the SW Baltic Sea, although seawater carbonate concentrations are permanently low and even seasonally undersaturated (Lutze, 1974; Wefer, 1976; Grobe and Fütterer, 1981; Polovodova et al., 2009; Thomsen et al., 2010; Haynert et al., 2011). Salinity, temperature, oxygen, and food availability were considered as important factors, which regulate the foraminiferal diversity and abundance (e.g. Rottgardt, 1952; Bradshaw, 1957; Lutze, 1965; Wefer, 1976; Alve and Murray, 1999; Frenzel et al., 2005). These studies, however, did not take into account the impact of seawater carbonate chemistry.

Living benthic foraminiferal assemblages in Flensburg Fjord were first described by Exon (1972). Some specimen of *Ammonia aomoriensis* from this area were reported as having thin or opaque shell walls and extremely corroded tests (Polovodova et al., 2009). In some cases, the tests were completely destroyed and only the inner organic lining was left. Abrasion and predation were considered as possible mechanisms for test destruction, but test dissolution due to fluctuated pH has been suggested as the most likely cause for the corroded *Ammonia* tests in that area (Polovodova and Schönfeld, 2008). Indeed, similar signs of test dissolution were observed, when living specimen of *Ammonia aomoriensis* from Flensburg Fjord were exposed to elevated

$p\text{CO}_2$ levels from 929 to 3130 μatm in a laboratory experiment (Haynert et al., 2011).

Natural CO₂-rich habitats can serve as valuable examples for possible effects on calcifying benthic community structures due to climate change (Hall-Spencer et al., 2008; Thomsen et al., 2010). Our study site in Flensburg Fjord, SW Baltic Sea represents an adequate study area for dynamic response of the foraminiferal fauna to elevated $p\text{CO}_2$. The consequences of naturally CO₂-enriched environments on benthic foraminifera are not sufficiently studied to date.

The aim of this study was to investigate the response of the foraminiferal population dynamics, as well as the variations of species composition and diversity to a high $p\text{CO}_2$ and low Ω_{calc} conditions over a one-year cycle. The main focus was on two calcifying species, *Ammonia aomoriensis* and *Elphidium incertum*. An effect of low sediment pore water carbonate saturation on population density and test dissolution of this species was assessed.

2 Study site and sampling

Flensburg Fjord, located in the southwest of the Baltic Sea (53°41'–55°00' N, 9°24'–10°10' E), is a narrow and 50 km long inlet. The Fjord is subdivided into a 10–20 m deep inner fjord which extends from the city Flensburg to Holnis Peninsula. The area from Holnis Peninsula to Neukirchen/Kragesand is a 18–20 m deep middle fjord. The 10–32 m deep outer fjord comprises Soenderborg Bay, Gelling Bay and open waters to the east of Gelling Peninsula.

Sediment and water samples were taken from seven stations (FF1 to FF7) on six bi-monthly cruises with R/V *Littorina* from June 2009 to April 2010 (Fig. 1). All seven stations (FF1 to FF7) were monitored for water carbonate chemistry. Sediment cores for foraminiferal studies were taken from stations FF1, FF4 and FF5. Station FF1 is located in a shallow near-coastal area, where sandy bottoms prevail (Table 1). At stations FF4 and FF5 muddy sands were encountered (Table 1). The cliff and submarine erosion are predominant sources for sediments, which are transported from the east by long shore drift toward the outer Flensburg Fjord (Exon, 1971).

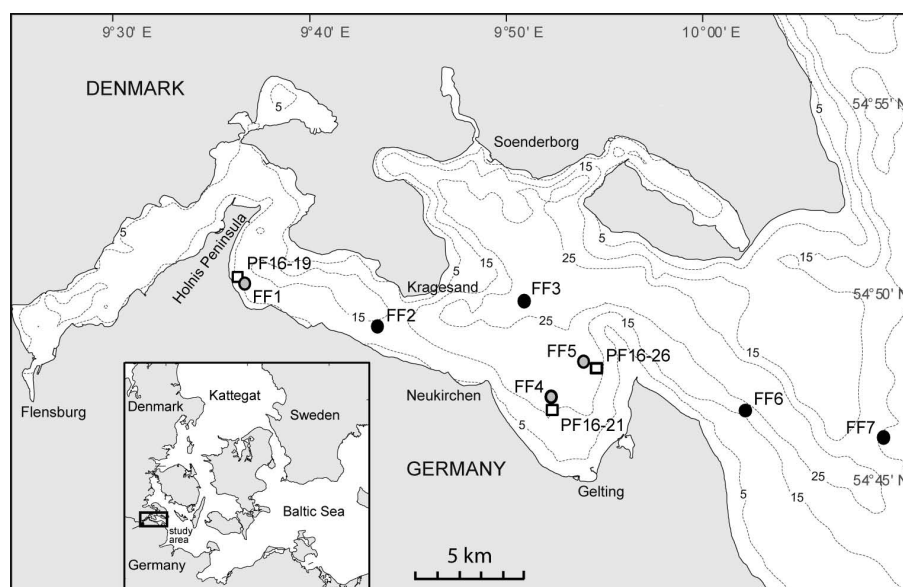
3 Material and methods

3.1 Foraminiferal processing

The foraminiferal communities were studied from surface sediments from stations FF1, FF4 and FF5. Benthic foraminiferal samples were taken with a Mini Muc K/MT 410 corer equipped with tubes of 60 cm length and 10 cm inner diameter. A plastic ring marked with 0.5 cm-scale was used to slice the uppermost one centimetre of the sediment core. A thin grey spatula was gently moved between tube top and the plastic ring. The surface layer (0–1 cm) of

Table 1. Sampling stations in Flensburg Fjord: specification, sampling device, latitude and longitude, water depth in metre, and sediment type at the corer stations (FF1, FF4 and FF5).

Station	Specification	Sampling device	Latitude [N]	Longitude [E]	Depth [m]	Sediment type
FF1	Corer station	MUC	54°50.50′	9°37.00′	13	sandy mud
PF16-19 (Polovodova and Schönfeld, 2008)	Corer station	Rumohr corer	54°50.20′	9°36.84′	10	sandy mud
FF2	Water chemistry station	CTD	54°49.00′	9°43.00′	18	–
FF3	Water chemistry station	CTD	54°50.00′	9°50.00′	27	–
FF4	Corer station	MUC	54°47.02′	9°51.37′	13	muddy sand
PF16-21 (Polovodova and Schönfeld, 2008)	Corer station	Rumohr corer	54°46.92′	9°51.26′	9	muddy sand
FF5	Corer station	MUC	54°48.02′	9°53.05′	13	muddy sand
PF16-26 (Polovodova and Schönfeld, 2008)	Corer station	Rumohr corer	54°48.28′	9°53.49′	8	muddy sand
FF6	Water chemistry station	CTD	54°47.00′	10°00.00′	22	–
FF7	Water chemistry station	CTD	54°46.00′	10°10.00′	23	–

**Fig. 1.** Map of study area of Flensburg Fjord (design by courtesy of Anna Nikulina, GEOMAR). Insert indicates the location of study area within the SW Baltic Sea. Circles display sediment corer (FF1, FF4 and FF5) and water chemistry stations (FF1–FF7). White squares indicate sampling stations PF16–19, PF16–21 and PF16–26 of Polovodova et al. (2009) in June 2006.

sediment was safely removed from the core and transferred with a spoon into 300 ml Kautex™ wide-neck containers. The sediment was preserved and stained with a Rose Bengal ethanol solution of 2 g l⁻¹ according to Lutze and Altenbach (1991). Ethanol concentration was 94 %. Staining time was three weeks at minimum, to ensure that the protoplasm was completely impregnated with Rose Bengal in all tests of foraminifera that were living at the time of sampling.

In the laboratory, samples were first passed through a 2000 µm screen in order to remove molluscs shells and pebbles. Subsequently the samples were gently washed with tap water through a 63-µm sieve. The fractions 63–2000 µm and > 2000 µm fractions were dried at 60 °C for at least 24 h. The fraction 63–2000 µm was split by using an Otto (1933) microsplitter to obtain aliquots of a manageable size. Subsequently, all size fractions were weighted and the fraction 63–2000 µm were quantitatively analysed for living and dead

foraminifera. All Rose Bengal stained foraminifera were considered as living at the time of sampling, whereas unstained tests were considered as dead. Living and dead specimens were picked from the respective aliquots, sorted by species, mounted in Plummer cell slides with glue, counted and measured. The dominant species were photographed by using a scanning electronic microscope (Cam Scan-CS-44) at the Institute of Geosciences, Kiel University.

In order to document the differences in test dissolution, foraminiferal tests were photographed using a scanning electronic microscope (Cam Scan-CS-44) and an electron probe microanalyser (Jeol JXA-8200 EPMA). Light micrographs were taken with a MiniPixie (MPX2051UC) digital microscope. The tests of living *A. aomoriensis* were subdivided into three dissolution stages: intact tests, dissolution of the last chamber, and dissolution of more than two chambers.

3.2 Carbonate chemistry

Temperature and salinity parameters of the surface and near-bottom water were recorded using a CTD48M probe (Sea & Sun Technology) at all stations (Tables 2 and 3). At water chemistry stations, samples for analyses of carbonate chemistry parameters were taken from the surface water at 1 m depth on stations FF1 to FF7 (Table 2), near-bottom water from 1 m above sea floor was taken at stations FF2, FF3, FF6 and FF7. Bottom water approximately 1 cm above the sediment surface and sediment pore water from 0 to 5 cm sediment depth was only collected at foraminifera sampling stations FF1, FF4 and FF5 (Table 3).

Surface and near-bottom water samples were taken using Niskin bottles and filled bubble free into 250 or 500 ml Duran™ glass bottles. Samples were poisoned with 50 or 100 µl saturated mercury chloride solution and stored at room temperature until analysis. Total alkalinity (A_T) and total inorganic carbon (C_T) of the samples were measured by potentiometric titration using VINDTA autoanalyser and coulometric titration after CO₂ extraction using the SOMMA system, respectively (Mintrop et al., 2000; Dickson et al., 2007). Offset of total alkalinity (A_T) and total carbon (C_T) determinations (Tables 2 and 3) were assessed and corrected by measurements of certified reference material (Dickson et al., 2003). Seawater pH_{NBS}, $p\text{CO}_2$ and omega for calcite (Ω_{calc}) were calculated by using the CO2Sys-program developed by Lewis and Wallace (1998) (Tables 2 and 3). Dissociation constants K_1 and K_2 were chosen according to Mehrbach et al. (1973) as refitted by Dickson and Millero (1987) and the KHSO₄ dissociation constant after Dickson (1990).

Bottom water samples for carbonate system parameters were taken from the supernatant water of Minicorer-tubes and filled directly into 20 ml PVC bottles. For sediment pore water analyses, the sediment cores were sliced in 0.5 cm intervals up to 2 cm depth, below 2 cm the intervals were 1.0 cm up to 5 cm. Sediment samples from each interval were transferred to 50 ml centrifuge tubes and centrifuged at 3000 rpm for 30 to 40 min in order to separate the sediment pore water from the sediment. The extracted sediment pore water and the bottom water were transferred through 0.2 µm steril filters into 20 ml PVC bottles. Bottom and sediment pore water pH_{NBS} were measured using a WTW 340i with a precision of ± 0.01. The pH electrode was calibrated using standard buffer solutions of pH 4.01, 7.00 and 10.00 (WTW standard, DIN/NIST buffers L7A). Subsequently, bottom and sediment pore water alkalinity was determined with a Metrohm titration instrument according to Ivanenkov and Lyakhin (1978). A greenish-brown Methyl-Red and Methylene-Blue indicator was added, and titration was performed with 0.02 M HCl and finished until a stable light pink colour occurred. During titration, the sample was degassed by continuously bubbling nitrogen through the solution in order to remove the generated CO₂ or H₂S. The

measured values were standardized using an IAPSO seawater solution. The precision of the alkalinity measurements was 0.37 %. The carbonate system parameters of bottom and sediment pore water, total carbon (C_T), $p\text{CO}_2$ and omega for calcite (Ω_{calc}) were calculated from measured pH_{NBS} and total alkalinity (A_T) according to dissociation constants as specified above.

4 Results

4.1 Temperature and salinity

Surface and near-bottom water temperature and salinity from stations FF1 to FF7 in Flensburg Fjord were characterised by pronounced seasonal fluctuations, prevailing in the area of the Baltic Sea. Temperature ranged from −0.9 to 20 °C at the surface and from −0.8 to 15.3 °C at the bottom during the investigation period (Tables 2 and 3).

A stable thermocline from 7 to 8 m water depth stratified the water column between June and August 2009. From December 2009 to April 2010, the water column was well mixed with a temperature of 5 °C on average in both, surface and near-bottom water. The surface of Flensburg Fjord was covered by floating ice in February, during that time the lowest temperatures were observed, ranging from −0.9 to 1.1 in the surface and near-bottom water (Tables 2 and 3).

Mean salinity ranged from 13.3 to 21.1 at the surface, and 16.8 to 26.3 in the bottom water (Tables 2 and 3). The salinity increased from the surface (15.7) to the near-bottom water (21.4), caused a persistent pycnocline from spring to summer. Mixing in October caused a homogenous salinity in the water column of approximately 22. A slight halocline in December caused again a lower mean salinity of 18.1 in the surface and a higher value of 22.8 in the bottom water (Tables 2 and 3). In February, the boundary layer between the surface and near-bottom water was dissipated and a uniform salinity of 17 was observed.

4.2 Carbonate chemistry

Carbonate chemistry measurements revealed a relatively stable surface $p\text{CO}_2$ during the whole year (Fig. 2a). In contrast, pH and $p\text{CO}_2$ in the bottom and sediment pore water showed a high variability during the seasonal cycle in Flensburg Fjord (Fig. 2b and c).

Surface $p\text{CO}_2$ ($478 \pm 197 \mu\text{atm}$) was close to atmospheric levels with slightly lower values during the spring bloom, similarly pH (8.13 ± 0.15) was relatively high and stable (Table 2, Fig. 2a). In general, the western Baltic Sea is characterised by a low salinity, ranging from 13 to 21, and consequently a low alkalinity (A_T) of 1821 to 2057 $\mu\text{mol kg}^{-1}$ prevailed in the surface water (Table 2). Consequently, the calcium carbonate saturation state for calcite (Ω_{calc}) was low in this area. During the monitoring, we recorded a mean surface Ω_{calc} of 1.84 ± 0.70 in 2009 and 2010. Undersaturation

Table 2. Flensburg Fjord surface seawater chemistry speciation 2009 to 2010 at the sampling stations (FF1–FF7). Temperature and salinity were recorded using a CTD48M probe. Analyses for total alkalinity (A_T) and dissolved inorganic carbon (C_T) were measured by coulometric and potentiometric titration using SOMMA and VINDTA systems. pH_{NBS} , carbon dioxide partial pressure ($p\text{CO}_2$) and omega of calcite (Ω_{calc}) were calculated using the CO2Sys-software.

Surface water							
Station	Temperature [°C]	Salinity	pH_{NBS}	A_T [$\mu\text{mol kg}^{-1}$]	C_T [$\mu\text{mol kg}^{-1}$]	$p\text{CO}_2$ [μatm]	Ω_{calc}
FF1 (1 m)							
02.06.2009	16.0	15.8	8.24	1933.3	1820.3	368	2.62
18.08.2009	17.7	18.6	8.05	1973.8	1891.6	585	2.05
20.10.2009	10.3	21.1	8.10	2056.8	1975.0	492	1.93
07.12.2009	6.7	17.3	8.09	1972.9	1923.8	499	1.45
15.02.2010							
19.04.2010	7.6	15.7	8.06	1900.4	1862.4	532	1.30
FF2 (1 m)							
02.06.2009	15.9	15.6	8.23	1918.5	1810.0	375	2.54
18.08.2009	17.8	18.6	8.19	1988.2	1862.7	410	2.78
20.10.2009	10.9	20.8	8.03	2038.0	1972.4	575	1.70
07.12.2009	6.8	17.4	8.08	1980.3	1932.0	509	1.44
15.02.2010	−0.8	17.2	7.66	1904.8	1972.0	1249	0.40
19.04.2010	7.8	15.2	8.20	1889.1	1822.2	380	1.72
FF3 (1 m)							
02.06.2009	16.3	15.4	8.21	1907.0	1805.4	398	2.42
18.08.2009	18.2	18.1	8.27	1976.8	1826.6	336	3.24
20.10.2009	10.7	20.7	8.10	2030.8	1948.1	484	1.93
07.12.2009	7.9	18.4	8.03	1982.4	1939.2	577	1.37
15.02.2010	−0.9	17.1	8.23	1952.5	1897.5	325	1.46
19.04.2010	7.4	15.0	8.30	1890.2	1800.5	294	2.10
FF4 (1 m)							
02.06.2009							
18.08.2009							
20.10.2009							
07.12.2009	7.8	18.6	8.03	1980.3	1936.5	576	1.37
15.02.2010	−0.8	17.1	7.78	1912.0	1950.6	941	0.53
19.04.2010	8.0	14.3	8.34	1882.2	1784.0	271	2.27
FF5 (1 m)							
02.06.2009							
18.08.2009							
20.10.2009	10.7	20.7	8.09	2032.0	1954.2	502	1.88
07.12.2009	8.0	18.6	7.99	1980.0	1943.0	622	1.29
15.02.2010	−0.8	17.1	7.85	1949.6	1974.7	820	0.62
19.04.2010	7.3	14.9	8.22	1874.8	1805.0	355	1.76
FF6 (1 m)							
02.06.2009	15.6	15.0	8.21	1881.6	1785.2	392	2.32
18.08.2009	18.6	17.0	8.29	1934.9	1787.9	325	3.23
20.10.2009							
07.12.2009	7.9	19.0	8.08	1993.5	1935.5	507	1.57
15.02.2010	−0.8	16.8	8.25	1936.4	1877.9	307	1.50
19.04.2010	6.7	13.3	8.32	1830.2	1749.3	281	1.96
FF7 (1 m)							
02.06.2009	14.5	15.1	8.22	1890.9	1796.0	385	2.28
18.08.2009	20.0	15.9	8.25	1893.9	1762.5	361	3.00
20.10.2009	10.8	19.9	8.23	1957.8	1845.9	346	2.37
07.12.2009	7.0	17.2	8.16	1926.1	1860.7	408	1.66
15.02.2010	−0.9	16.2	8.05	1903.7	1889.0	495	0.94
19.04.2010	6.7	13.9	8.12	1821.0	1781.7	455	1.29

Table 3. Water chemistry parameters of the near-bottom water (1 m above the sea floor) at stations FF2, FF3, FF6 and FF7 and of the bottom water (1 cm above the sediment surface) at stations FF1, FF4 and FF5 from June 2009 to April 2010. Temperature and salinity were measured by CTD48M probe at all stations from FF1 to FF7. At stations FF1, FF4 and FF5, the bottom water pH_{NBS} were measured using a WTW 340i. Analysis of total alkalinity (A_T) was determined with a Metrohm titration instrument. Dissolved inorganic carbon (C_T), carbon dioxide partial pressure (pCO_2), and omega calcite (Ω_{calc}) were calculated using the CO2Sys-program. At stations FF2, FF3, FF6 and FF7, analyses for total alkalinity (A_T) and dissolved inorganic carbon (C_T) were measured by coulometric and potentiometric titration using SOMMA and VINDTA systems. pH_{NBS}, carbon dioxide partial pressure (pCO_2) and omega of calcite (Ω_{calc}) were calculated using the CO2Sys-software.

Near-bottom and bottom water							
Station	Temperature [°C]	Salinity	pH _{NBS}	A_T [$\mu\text{mol kg}^{-1}$]	C_T [$\mu\text{mol kg}^{-1}$]	pCO_2 [μatm]	Ω_{calc}
Bottom water FF1 (13 m)							
02.06.2009	13.2	19.9	7.63	2388.4	2385.6	1337	1.19
18.08.2009	14.6	20.0	7.54	2199.5	2213.7	1536	0.95
20.10.2009	10.5	21.0	7.29	2465.7	2581.7	3074	0.53
07.12.2009	9.1	21.5	7.84	2174.0	2126.6	700	1.51
15.02.2010							
19.04.2010	5.7	18.7	7.86	2353.5	2322.2	739	1.41
Near-bottom water FF2 (18 m)							
02.06.2009	7.2	21.2	7.86	2060.1	2046.6	857	1.04
18.08.2009	11.6	21.6	7.40	2079.7	2173.1	2661	0.45
20.10.2009	11.0	21.4	7.93	2073.6	2030.7	754	1.40
07.12.2009	9.2	23.0	7.98	2053.7	1998.2	631	1.52
15.02.2010	-0.8	17.2	8.03	1951.5	1938.3	529	0.94
19.04.2010	4.3	19.4	8.03	2023.9	1987.5	557	1.26
Near-bottom water FF3 (27 m)							
02.06.2009	7.4	23.5	7.92	2123.3	2085.1	735	1.32
18.08.2009	11.1	23.4	7.45	2117.9	2193.1	2348	0.53
20.10.2009	13.2	23.4	7.49	2093.6	2149.8	2168	0.61
07.12.2009	9.0	24.0	8.02	2076.3	2006.2	568	1.70
15.02.2010	-0.2	17.5	8.08	1985.8	1958.9	478	1.11
19.04.2010	2.7	22.4	7.55	2022.4	2095.3	1631	0.45
Bottom water FF4 (13 m)							
02.06.2009	15.1	20.4	7.52	2367.3	2350.3	1267	1.34
18.08.2009	12.8	21.1	7.43	2236.1	2283.7	1982	0.72
20.10.2009	11.2	22.4	7.21	2360.4	2491.4	3429	0.45
07.12.2009	8.6	24.1	7.85	2187.8	2131.2	673	1.60
15.02.2010	-0.4	16.8	7.81	1816.8	1823.3	634	0.70
19.04.2010	4.8	19.0	7.88	2234.5	2201.5	655	1.35
Bottom water FF5 (13 m)							
02.06.2009	10.3	20.2	7.83	2125.5	2082.8	727	1.45
18.08.2009	15.3	19.8	7.47	2239.1	2270.8	1861	0.85
20.10.2009	11.9	21.6	7.29	2465.7	2573.0	3083	0.57
07.12.2009	8.8	20.9	7.81	2174.0	2138.9	769	1.36
15.02.2010	-0.4	16.9	7.94	1804.6	1784.3	465	0.98
19.04.2010	5.6	18.8	7.94	2374.9	2321.6	604	1.70
Near-bottom water FF6 (22 m)							
02.06.2009	7.6	22.0	7.87	2070.3	2051.0	843	1.10
18.08.2009	11.2	23.8	7.50	2115.9	2175.3	2091	0.59
20.10.2009							
07.12.2009	9.0	23.5	8.01	2056.1	1992.4	585	1.62
15.02.2010	-0.8	17.2	8.19	1960.1	1913.6	362	1.34
19.04.2010	2.9	21.4	7.68	2038.9	2081.0	1248	0.59
Near-bottom water FF7 (23 m)							
02.06.2009	8.7	26.3	7.87	2082.3	2043.1	796	1.30
18.08.2009	11.9	22.9	7.46	2089.3	2161.3	2326	0.53
20.10.2009	13.4	24.7	8.00	1985.0	1904.1	588	1.84
07.12.2009	9.0	22.9	8.02	2050.6	1986.8	577	1.62
15.02.2010	1.1	18.6	7.96	1974.5	1964.2	624	0.93
19.04.2010	2.9	22.8	7.63	2072.0	2122.5	1379	0.56

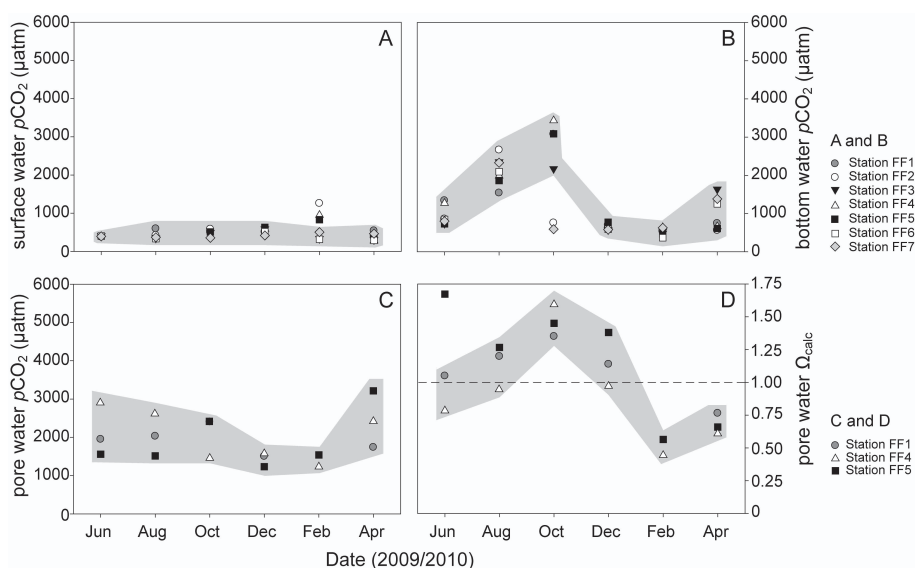


Fig. 2. (A and B) surface water, near-bottom water, and bottom water $p\text{CO}_2$ at sampling stations from FF1 to FF7; (C and D) sediment pore water $p\text{CO}_2$ and Ω_{calc} at stations FF1, FF4 and FF5 from June 2009 to April 2010.

of the surface water was observed in February, with Ω_{calc} values ranging from 0.40 to 0.94 (Table 2).

Stratification of the water column causes a strong CO₂-accumulation in the bottom water during summer and autumn. Therefore, large seasonal fluctuations of $p\text{CO}_2$, pH and Ω_{calc} were observed in the near-bottom and bottom water. One metre above the sediment, the mean near-bottom water $p\text{CO}_2$ was $1120 \pm 82.86 \mu\text{atm}$. In comparison, the bottom water $p\text{CO}_2$ (1 cm above sediment) increased to $1390 \pm 71.63 \mu\text{atm}$ (Table 3). Highest $p\text{CO}_2$ levels reached up to $2000 \mu\text{atm}$ during August in the near-bottom water and up to $3000 \mu\text{atm}$ during October in the bottom water a few cm above the benthic boundary (Table 3, Fig. 2b). This caused lowest pH values of 7.40 and 7.21 in the near-bottom and bottom waters during August and October (Table 3). After mixing of the water column, $p\text{CO}_2$ decreased in winter to mean values of $550 \pm 65.44 \mu\text{atm}$ and 657 ± 132.07 (Table 3). Similarly, mean pH showed the highest value of 7.91 in the near-bottom water and 7.85 in the bottom water (Table 3). The calculated mean Ω_{calc} values in the near-bottom water (1.08 ± 0.07) and bottom water (1.10 ± 0.05) were low compared to surface Ω_{calc} and varied between the studied stations (Table 3). The near-bottom and bottom waters of Flensburg Fjord were frequently undersaturated for Ω_{calc} with a lowest value of 0.45 in August and October (Table 3).

The carbonate chemistry of the sediment pore waters strongly deviated from the conditions in the water column. Sediment pore water $p\text{CO}_2$ from the depth-interval 0 to 1 cm, did not fluctuate as strong as the bottom water. It was noticeable that the $p\text{CO}_2$ was high during the whole year and ranged from 1244 to $3324 \mu\text{atm}$ (Table 4, Fig. 2c). Mean sediment pore water $p\text{CO}_2$ of the 0–1 cm depth-interval was

$2013 \pm 610 \mu\text{atm}$, pH (7.55 ± 0.10) was lower, but more stable in comparison to the water column (Table 4, Fig. 2c). In contrast, the pH-profile of the sediment pore water revealed considerable fluctuations within the 1 and 5 cm depth-interval, ranging from 6.82 to 8.11 (Fig. 3). Furthermore, the pH-fluctuations varied also between the sampling stations and during the seasonal cycle. No trend was observed in the 5 cm depth-interval. Compared to the bottom water A_T ($2233 \pm 190 \mu\text{mol kg}^{-1}$), the sediment pore water alkalinity was much higher ($2856 \pm 400 \mu\text{mol kg}^{-1}$) which causes a relative high, slightly supersaturated Ω_{calc} of 1.09 ± 0.38 (Table 4, Fig. 2d). Only sediments at station FF4 were consistently undersaturated for Ω_{calc} with the lowest value of 0.46 in February (Table 4, Fig. 2d).

4.3 Foraminiferal population density and species composition

Population density of the living foraminiferal fauna in Flensburg Fjord ranged from 15 to $223 \text{ ind. } 10 \text{ cm}^{-3}$, on average $68 \text{ ind. } 10 \text{ cm}^{-3}$. The abundance of dead specimens ranged from 16 to $454 \text{ tests } 10 \text{ cm}^{-3}$, on average $127 \text{ tests } 10 \text{ cm}^{-3}$. The assemblages consisted of six calcareous species: *Ammonia aomoriensis*, *Elphidium albiumbilicatum*, *Elphidium excavatum clavatum*, *Elphidium excavatum excavatum*, *Elphidium gerthi* and *Elphidium incertum*, and two arenaceous species *Ammotium cassis* and *Reophax dentaliniformis* (Fig. 6). Foraminiferal faunas were dominated by *A. aomoriensis*, *E. incertum* and *A. cassis* (Fig. 4). The specimens of common to rare species, which were occasionally present in the foraminiferal assemblages, were combined to one group, called “Other” (Tables 5 and 6).

Table 4. Seawater carbonate chemistry of bottom water (1 cm above the sediment surface) and sediment pore water (0–1 cm) at stations FF1, FF4 and FF5 during the one year cycle. Bottom and sediment pore water pH_{NBS} were measured using a WTW 340i. Total alkalinity (A_T) was determined with a Metrohm titration instrument. Dissolved inorganic carbon (C_T), carbon dioxide partial pressure (pCO_2), and omega calcite (Ω_{calc}) were calculated using the CO2Sys-software.

Station	bottom water pH _{NBS}	sediment pore water 0–1 cm pH _{NBS}	bottom water A_T [$\mu\text{mol kg}^{-1}$]	sediment pore water 0–1 cm A_T [$\mu\text{mol kg}^{-1}$]	bottom water C_T [$\mu\text{mol kg}^{-1}$]	sediment pore water 0–1 cm C_T [$\mu\text{mol kg}^{-1}$]	bottom water pCO_2 [μatm]	sediment pore water 0–1 cm pCO_2 [μatm]	bottom water Ω_{calc}	sediment pore water 0–1 cm Ω_{calc}
FF1										
02.06.2009	7.63	7.52	2388.4	2684.3	2385.6	2716.3	1337	1968	1.19	1.07
18.08.2009	7.54	7.53	2199.5	2833.6	2213.7	2858.8	1536	2058	0.95	1.22
20.10.2009	7.29	7.54	2465.7	3576.4	2581.7	3623.9	3074	2433	0.53	1.38
07.12.2009	7.84	7.61	2174.0	2694.9	2126.6	2709.8	700	1512	1.51	1.15
15.02.2010										
19.04.2010	7.86	7.54	2353.5	2610.3	2322.2	2668.7	739	1746	1.41	0.77
FF4										
02.06.2009	7.52	7.36	2367.3	2726.6	2350.3	2806.8	1267	2965	1.34	0.80
18.08.2009	7.43	7.44	2236.1	2995.1	2283.7	3063.5	1982	2699	0.72	0.98
20.10.2009	7.21	7.69	2360.4	3062.2	2491.4	3050.2	3429	1709	0.45	1.76
07.12.2009	7.85	7.55	2187.8	2577.7	2131.2	2604.3	673	1631	1.60	0.99
15.02.2010	7.81	7.56	1816.8	2067.4	1823.3		634	1292	0.70	0.46
19.04.2010	7.88	7.43	2234.5	2861.0	2201.5	2972.4	655	2494	1.35	0.64
FF5										
02.06.2009	7.83	7.69	2125.5	3281.1	2082.8	3274.1	727	1573	1.45	1.69
18.08.2009	7.47	7.60	2239.1	2496.7	2270.8	2494.8	1861	1545	0.85	1.29
20.10.2009	7.29	7.54	2465.7	3576.4	2573.0	3613.7	3083	2437	0.57	1.49
07.12.2009	7.81	7.70	2174.0	2740.2	2138.9	2731.1	769	1244	1.36	1.39
15.02.2010	7.94	7.61	1804.6	2494.0	1784.3		465	1593	0.98	0.63
19.04.2010	7.94	7.42	2374.9	3273.5	2321.6	3421.6	604	3324	1.70	0.78

Calculations of two diversity indices, Shannon-Wiener-Index and Fishers alpha, exhibited low values at all stations which indicates a low diversity of living and dead assemblages. There is a maximum of 8 species constituting the community. Hence, any changes in assemblages composition will induce only insignificant differences of diversity.

4.3.1 Living assemblages

Stations FF1 and FF5 showed a similar trend of population density and composition of living species during the seasonal cycle (Fig. 4). FF1 is located in the middle part of the fjord, where the sediment consists of sandy mud, whereas station FF5 is located in the outer fjord of Flensburg where muddy sand prevailed (Fig. 1). Maximum numbers of 101 and 129 ind. 10 cm⁻³ were observed in October at stations FF1 and FF5, when *A. aomoriensis* was frequent with 49 and 72 % (Fig. 4, Table S1 in the Supplement). At station FF1, *A. aomoriensis* was also frequent in April with 61 %, and it was common with 17 % in August. *Elphidium incertum* dominated with 52 and 48 % during summer, and *A. cassis* was rather rare with 1 % (Fig. 4, Table S1 in the Supplement). In contrast, *E. incertum* was the dominant species with 34 %

on average during the whole year at station FF5 (Table 5). The arenaceous species *A. cassis* was very frequent in August and in February with 63 and 37 % (Table 5). At station FF4, which was also located in the outer Fjord, *E. incertum* was the dominant species during the whole year and showed a maximum of 94 % in April. In comparison, *A. aomoriensis* was rare, ranging from 0 to 9 % (Fig. 4). *A. cassis* achieved maximum proportions of 36 % in December (Table 5).

4.3.2 Dead assemblages

During the whole investigation period (except of June at FF4 and FF5), *A. aomoriensis* dominates the dead assemblages at stations FF1, FF4 and FF5 with 62, 46 and 39 % on average (Table S1 in the Supplement, Fig. 4). At station FF1, abundance of dead foraminifera was consistently higher ranging from 118 to 454 tests 10 cm⁻³ in comparison to the other stations. At station FF1, *E. incertum* was common with 14 %, and *A. cassis* was very rare with 0.4 % on average throughout the year (Fig. 4). In contrast, *E. incertum* was common at stations FF4 and FF5, and depicted maximum values in February and April with 42 % on average at station FF4 (Table 6). The arenaceous species *A. cassis* was frequent with

Table 5. List of living foraminiferal assemblages collected at the studied stations (FF1, FF4 and FF5) of Flensburg Fjord between June 2009 and April 2010, size fraction 63–2000 µm.

Station	Living foraminiferal species 0–1 cm > 63 µm	June		August		October		December		February		April	
		02.06.2009	%	18.08.2009	%	20.10.2009	%	07.12.2009	%	15.02.2010	%	19.04.2010	%
Station FF1	Species												
	<i>Ammonia aomoriensis</i>	25	25.3	37	16.7	132	48.7	23	43.4			69	61.1
	<i>Elphidium albibiblicatum</i>	1	1.0	2	0.9	42	15.5	2	3.8			1	0.9
	<i>Elphidium excavatum clavatum</i>	5	5.1	28	12.7	53	19.6	4	7.5			7	6.2
	<i>Elphidium excavatum excavatum</i>	16	16.2	33	14.9	24	8.9	16	30.2			18	15.9
	<i>Elphidium gerthi</i>	1	1.0	16	7.2								
	<i>Elphidium incertum</i>	51	51.5	105	47.5	12	4.4	8	15.1			16	14.2
	Total number of calcareous individuals	99		221		263		53				111	
	<i>Ammonium cassis</i>												
	<i>Reophax dentaliniformis</i>					8	3.0					1	0.9
Total number of agglutinated individuals	0		0		8		0				2		
Total number of living specimens	99		221		271		53				113		
Species number	6		6		6		5				7		
Sample volume (cm ³)	47		76		56		60				94		
Split (n)	0.5252		0.4585		0.4802		0.4791				0.5210		
Population density (ind. 10 cm ⁻³)	40.1		63.4		100.8		18.4				23.1		
Station FF4	Species												
	<i>Ammonia aomoriensis</i>	3	8.3	9	9.3	2	2.6	4	4.5			2	1.1
	<i>Elphidium albibiblicatum</i>			4	4.1								
	<i>Elphidium excavatum clavatum</i>			11	11.3	1	1.3						
	<i>Elphidium excavatum excavatum</i>			19	19.6	1	1.3						
	<i>Elphidium gerthi</i>												
	<i>Elphidium incertum</i>	28	77.8	51	52.6	57	74.0	52	59.1			160	92.0
	Total number of calcareous individuals	31		94		61		56				162	
	<i>Ammonium cassis</i>	2	5.6	1	1.0	15	19.5	32	36.4			12	6.9
	<i>Reophax dentaliniformis</i>	3	8.3	2	2.1	1	1.3					5	6.1
Total number of agglutinated individuals	5		3		16		32				12		
Total number of living specimens	36		97		77		88				174		
Species number	4		7		6		3				3		
Sample volume (cm ³)	59		95		100		93				73		
Split (n)	0.0663		0.2351		0.5080		0.4769				0.4913		
Population density (ind. 10 cm ⁻³)	92.0		43.4		15.2		19.8				48.5		
Station FF5	Species												
	<i>Ammonia aomoriensis</i>	13	14.9	12	7.0	63	72.4	64	28.6			6	6.6
	<i>Elphidium albibiblicatum</i>	8	9.2	2	1.2	2	2.3	19	8.5			1	1.1
	<i>Elphidium excavatum clavatum</i>	12	13.8			3	3.4	24	10.7			1	1.1
	<i>Elphidium excavatum excavatum</i>	29	33.3	4	2.3	12	13.8	63	28.1			2	2.2
	<i>Elphidium gerthi</i>	1	1.1			3	3.4					1	1.1
	<i>Elphidium incertum</i>	18	20.7	44	25.7	4	4.6	50	22.3			47	51.6
	Total number of calcareous individuals	81		62		87		221				56	
	<i>Ammonium cassis</i>	1	1.1	108	63.2			1	0.4			34	37.4
	<i>Reophax dentaliniformis</i>	5	5.7	1	0.6			2	0.9			1	1.1
Total number of agglutinated individuals	6		109		0		3				35		
Total number of living specimens	87		171		87		224				91		
Species number	8		6		6		8				6		
Sample volume (cm ³)	47		67		51		64				76		
Split (n)	0.1239		0.5340		0.1324		0.5071				0.5456		
Population density (ind. 10 cm ⁻³)	149.3		47.8		128.9		69.0				21.9		

Table 6. Foraminiferal census data of dead species collected at the studied stations (FF1, FF4 and FF5) of Flensburg Fjord between June 2009 and April 2010, size fraction 63–2000 µm.

Station	Dead foraminiferal species 0–1 cm > 63 µm	June 2009		August 2009		October 2009		December 2009		February 2010		April 2010	
		June 2009	%	August 2009	%	October 2009	%	December 2009	%	February 2010	%	April 2010	%
Station FF1	Species												
	<i>Ammonia aomoriensis</i>	343	72.2	941	59.5	213	54.9	377	59.1			369	64.1
	<i>Elphidium albimiblicatum</i>	1	0.2	3	0.2			2	0.3			2	0.3
	<i>Elphidium excavatum clavatum</i>	29	6.1	115	7.3	61	15.7	56	8.8			42	7.3
	<i>Elphidium excavatum excavatum</i>	8	1.7	183	11.6	68	17.5	114	17.9			92	16.0
	<i>Elphidium gerthi</i>	2	0.4			1	0.3	2	0.3				
	<i>Elphidium incertum</i>	87	18.3	296	18.7	38	9.8	63	9.9			64	11.1
	Total number of calcareous individuals	470		1538		381		614				569	
	<i>Ammonium cassis</i>	4	0.8	10	0.6			3	0.5			1	0.2
	<i>Reophax dentaliniformis</i>	1	0.2	33	2.1	7	1.8	21	3.3			6	1.0
	Total number of agglutinated individuals	5		43		7		24				7	
	Total number of specimens	475		1581		388		638				576	
	Species number	8		7		6		8				7	
Sample volume (cm ³)	47		76		56		60				94		
Split (n)	0.5252		0.4585		0.4802		0.4791				0.5210		
Abundance (tests 10 cm ⁻³)	192.4		453.7		144.3		221.9				117.6		
Station FF4	Species												
	<i>Ammonia aomoriensis</i>	1	8.3	19	52.8	142	49.1	353	85.9			38	40.4
	<i>Elphidium albimiblicatum</i>			3	8.3	8	2.8					2	2.1
	<i>Elphidium excavatum clavatum</i>	3	25.0	4	11.1	1	0.3						
	<i>Elphidium excavatum excavatum</i>	1	2.8	1	2.8								
	<i>Elphidium gerthi</i>	1	8.3	1	2.8	55	19.0	26	6.3			38	40.4
	<i>Elphidium incertum</i>	5		28		206		379				78	
	Total number of calcareous individuals	6	50.0	6	16.7	63	21.8	11	2.7			9	9.6
	<i>Ammonium cassis</i>	1	8.3	2	5.6	20	6.9	21	5.1			7	7.4
	<i>Reophax dentaliniformis</i>	7		8		83		32				16	
	Total number of agglutinated individuals												
	Total number of specimens	12		36		289		411				94	100
	Species number	5		7		6		4				5	4
Sample volume (cm ³)	59		95		100		93				73		
Split (n)	0.0663		0.2351		0.5080		0.4769				0.4913		
Abundance (tests 10 cm ⁻³)	30.7		16.1		56.9		92.7				26.2		
Station FF5	Species												
	<i>Ammonia aomoriensis</i>	3	12.5	279	43.5	23	62.2	94	39.8			32	45.8
	<i>Elphidium albimiblicatum</i>	1	4.2	11	1.7			2	0.8			2	0.3
	<i>Elphidium excavatum clavatum</i>	2	8.3	196	30.6	8	21.6	100	42.4			292	40.8
	<i>Elphidium excavatum excavatum</i>	10	41.7	4	0.6	2	5.4	1	0.4			3	1.5
	<i>Elphidium gerthi</i>		0.0					1	0.4				
	<i>Elphidium incertum</i>	7	29.2	137	21.4	3	8.1	33	14.0			53	26.1
	Total number of calcareous individuals	23		627		36		231				684	
	<i>Ammonium cassis</i>	1	4.2	6	0.9			2	0.8			22	3.1
	<i>Reophax dentaliniformis</i>			8	1.2	1	2.7	3	1.3			10	1.4
	Total number of agglutinated individuals												
	Total number of specimens	24		641		37		236				716	
	Species number	6		7		5		8				6	
Sample volume (cm ³)	47		67		51		64				76		
Split (n)	0.1239		0.5340		0.1324		0.5071				0.5456		
Abundance (tests 10 cm ⁻³)	41.2		179.2		54.8		72.7				172.7		

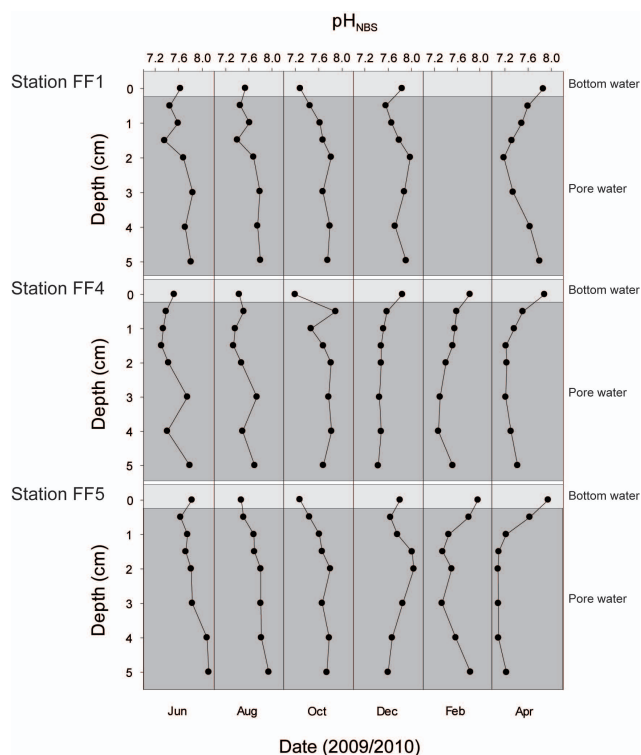


Fig. 3. Bottom and sediment pore water profiles of pH_{NBS} plotted vs. sediment depth (cm) at stations FF1, FF4 and FF5 during the seasonal cycle (2009/2010).

50 % in June at station FF4, otherwise it was rare with 2 % on average at station FF5 (Table 6).

4.4 Co-variance of population density with respect to carbonate chemistry

The living and dead foraminiferal assemblages fluctuated seasonally. In particular the population density of the living fauna suggests a certain co-variance with pore water $p\text{CO}_2$. However, scale and magnitude of the fluctuation in both parameters revealed that the population density was not directly affected by changing pore water $p\text{CO}_2$, respectively Ω_{calc} (Fig. S1 in the Supplement).

We tested the co-variance of the arenaceous species *A. cassis* and saturation state, but no correlation was recognised. The data provided no evidence that *A. cassis* could be affected by changing carbonate chemistry. Therefore, we will focus on the calcareous species, which directly respond to changes of the carbonate chemistry.

Living calcareous *A. aomoriensis* and *E. incertum* revealed mean population densities of 16 ind. 10 cm^{-3} and 33 ind. 10 cm^{-3} . No correlation with the sediment pore water $p\text{CO}_2$ was recognised, neither in the living assemblages (Fig. 5), nor in the dead assemblages (Fig. S2 in the Supplement). Furthermore, mean test diameter of living and dead

A. aomoriensis also exhibited no relationship between test size and $p\text{CO}_2$ (Table S2 in the Supplement).

In contrast to $p\text{CO}_2$, population densities of living *A. aomoriensis* showed a co-variance with saturation state Ω_{calc} . Mean population density was comparatively low (5 ind. 10 cm^{-3}) when undersaturated conditions from 0.46 to 0.99 prevailed (Fig. 5). It was noticeable that station FF4 exhibited undersaturated conditions in sediment pore waters with an Ω_{calc} between 0.46 and 0.99 during the whole year, with the exception of October with Ω_{calc} of 1.76 (Table 4). During that time however, *A. aomoriensis* showed the lowest population density of 3 ind. 10 cm^{-3} (Fig. 5; A). By comparison, stations FF1 and FF5 were most of the time supersaturated for Ω_{calc} from 1.07 to 1.69 (Table 4), and revealed mean population densities of 19 ind. 10 cm^{-3} and 35 ind. 10 cm^{-3} , respectively (Fig. 5; A).

In contrast, the population density of *E. incertum* showed no co-variance with sediment pore water Ω_{calc} . Under supersaturated Ω_{calc} conditions, the mean population density was lower with 15 ind. 10 cm^{-3} , in comparison to undersaturated values of Ω_{calc} with a population density of 53 ind. 10 cm^{-3} , on average (Fig. 5; C).

4.5 Tests of living calcareous foraminifera

The test walls of the dominant calcareous species *A. aomoriensis* and *E. incertum* were examined. Different stages of tests of *A. aomoriensis* were classified as (1) intact tests (Fig. 6: 2), (2) dissolution of the last chamber (Fig. 7a: 4) and (3) dissolution of more than two chambers (Fig. 7a: 5). Sixty four percent of the tests of living *A. aomoriensis* were intact and had a smooth and shiny surface, which was recognised in all samples during the one-year cycle (Fig. 6: 2). However, the remaining *A. aomoriensis* specimens exhibit different stages of test dissolution. At stations FF1 and FF5, 33 and 29 % of *A. aomoriensis* specimens exhibited dissolution of the last chamber. Dissolution of more than two chambers was observed in 4 and 13 % of the living specimens. All chambers were decalcified and in few individuals, only the inner organic lining was left.

In contrast, living *E. incertum* displayed no signs of dissolution. Occasionally, the last chambers of *E. incertum* were broken, which indicates impacts of mechanical forces, probably during sampling or processing (Fig. 7b: 6).

Furthermore, some test walls of living *A. aomoriensis* exhibited recalcified structures (Fig. 7b: 1–3). This recalcification was usually characterised by test deformities such as an irregular test shape (Fig. 7b: 2–3). The walls of the chambers were not completely covered by a newly formed calcite lamella, which indicated a fragmentary precipitation of calcite from the external to the internal test walls (Fig. 7b: 2). Old or compact and young or thinner chambers showed the same porosity (Fig. 7b: 2).

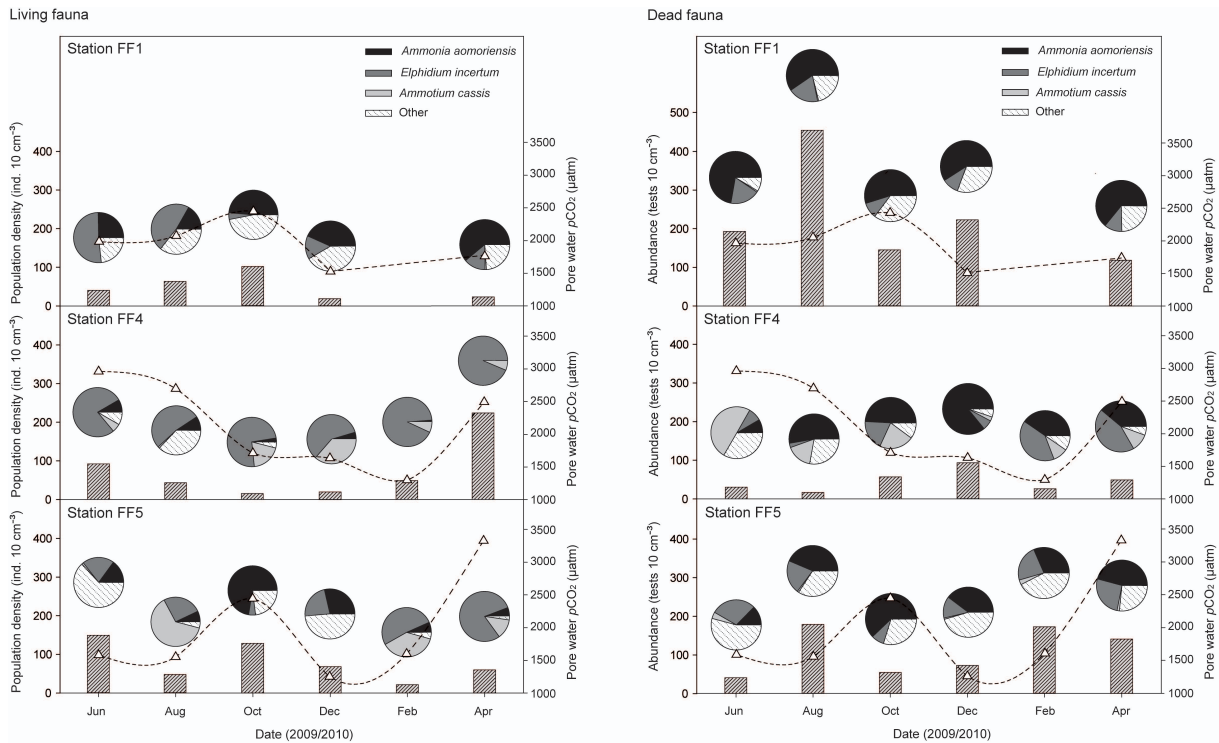


Fig. 4. Proportions and abundance of living and dead benthic foraminiferal species at stations FF1, FF4 and FF5 from June 2009 to April 2010. The bars present the population density and abundance of the living and dead fauna. Pie charts indicate the percentages of dominant species (Tables 5 and 6). Sediment pore water $p\text{CO}_2$ in Flensburg Fjord is displayed by white triangles.

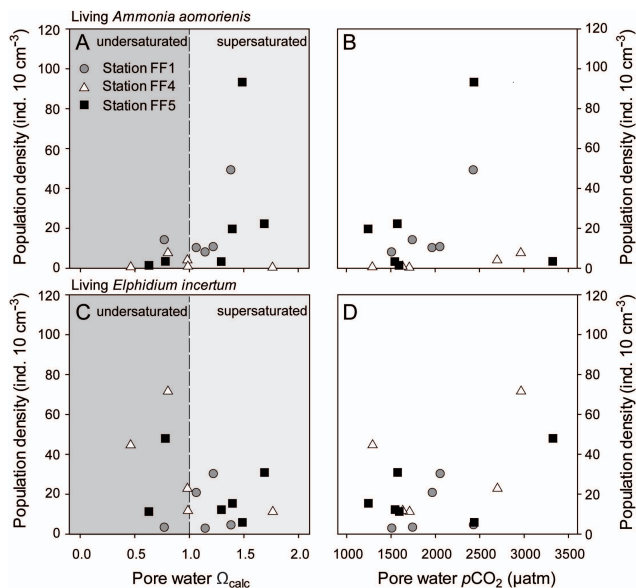


Fig. 5. Population density of living *A. aomoriensis* (A and B) and *E. incertum* (C and D) vs. sediment pore water Ω_{calc} (A and C) and $p\text{CO}_2$ (B and D). The different symbols present stations FF1, FF4 and FF5 during the one year cycle.

5 Discussion

5.1 Carbonate chemistry in Flensburg Fjord

Whereas, the surface $p\text{CO}_2$ of Flensburg Fjord is close to the atmospheric CO_2 concentrations, bottom water conditions were much more variable during the seasonal cycle. This seasonal variability of the carbonate chemistry is also found elsewhere in near coastal marine systems (Borges and Frankignoulle, 1999; Borges et al., 2006; Provoost et al., 2010; Thomsen et al., 2010; Hofmann et al., 2011).

These natural fluctuations are common in eutrophicated coastal habitats and estuaries (Diaz and Rosenberg, 2008; Conley et al., 2009; Nikulina and Dullo, 2009; Thomsen et al., 2010; Melzner et al., 2012). Furthermore, carbonate chemistry of the sediment pore water, especially in the living benthic foraminiferal habitat from 0–1 cm, strongly deviated from the conditions in the bottom water. Sediment pore water exhibited perennial high $p\text{CO}_2$ values ranging from 1244 to 3324 μatm . This is a consequence of C_T accumulation in the hypoxic water column and the surface sediments by aerobic processes. In contrast, in the deeper, anoxic sediments anaerobic bacterial decay of organic matter leads to production of metabolic bicarbonate (HCO_3^-) by nitrate and sulfate reduction and an increase of A_T (Yao and Millero, 1995). Whereas the HCO_3^- remains in the sediments, the gaseous

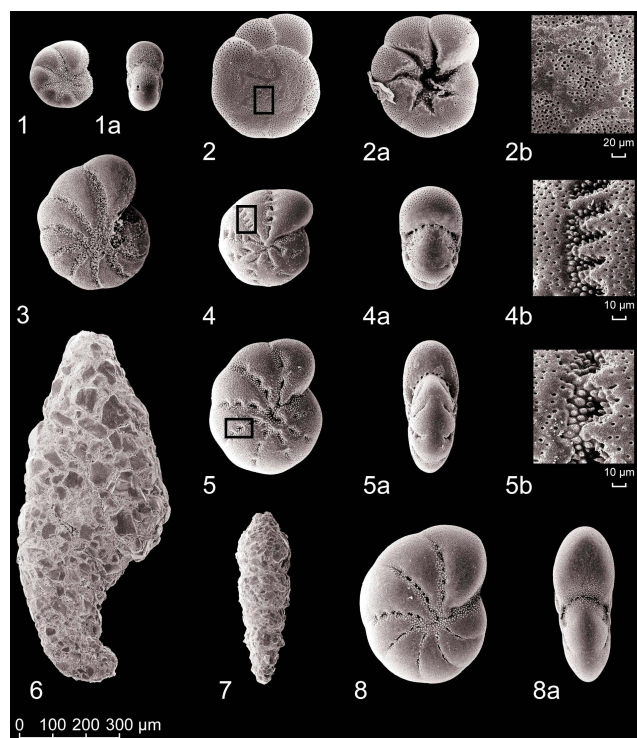


Fig. 6. Benthic foraminifera from Flensburg Fjord. 1 *Elphidium al-biumbilicatum*: spiral (1) and apertural (1a) views; 2 *Ammonia aomoriensis*: spiral (2), umbilical (2a) and detailed view of the test wall (2b); 3 *Elphidium gerthi*: spiral view; 4 *Elphidium excavatum clavatum*: spiral (4), apertural (4a) and detailed view of the suture of two chambers (4b); 5 *Elphidium excavatum excavatum*: spiral (5), apertural (5a) and detailed view of the suture of two chambers (5b); 6 *Ammotium cassis*: top view; 7 *Reophax dentaliniformis*: top view; 8 *Elphidium incertum*: spiral (8) and apertural (8a) views.

end products H₂S or N₂ are either degassing or are bound as iron sulphides (Kristensen et al., 1998; Thomas et al., 2009).

The A_T in the surface waters ranges from 1800 to 2100 $\mu\text{mol kg}^{-1}$ and thus is slightly lower than the buffer capacity of bottom water A_T (1800–2500 $\mu\text{mol kg}^{-1}$). However, the sediment pore water habitat of the benthic foraminifera exhibited a much higher alkalinity ranging from 2000 to 3500 $\mu\text{mol kg}^{-1}$. Remineralisation products cause C_T and A_T enriched sediment pore waters and an enhanced CO₂ buffer capacity (Thomas et al., 2009). Consequently, Ω_{calc} of the sediment pore waters was much higher than in the water column for most of the year. In contrast to stations FF1 and FF5, Ω_{calc} of station FF4 was undersaturated during most of the year. Both stations, FF4 and FF5, are located in Gelting Bay and have the same sediment, which is muddy sand. However, even slight differences in the sediment composition might cause different remineralisation processes (Kristensen et al., 1998; Asmus et al., 1998a,b), which could explain the Ω_{calc} undersaturation at station FF4.

5.2 Foraminiferal community

The population density of the living assemblages showed fluctuations which can be attributed to the seasonality of food supply and degradation of organic matter (Schönfeld and Numberger, 2007a). In particular, high values of food supply during April and October could mirror spring and autumn blooms. The subsequent flux of algal debris to the sea floor is the dominating parameter structuring the population density and species composition of benthic foraminiferal faunas (Altenbach et al., 1999; Morigi et al., 2001; Gooday, 2003). As such, it is conceivable that enhanced influx of organic matter provided sufficient food for a rich benthic community in Flensburg Fjord.

The composition of living and dead assemblages showed no correlation with $p\text{CO}_2$, respectively Ω_{calc} . This infers that either no extensive mortality occurred or dissolution of shells is prevented by the relative high carbonate saturation. Further, any shell loss of dead assemblages due to dissolution in seasonal undersaturated sediment pore waters was instantly compensated for by the delivery of empty tests from the living population through manifold reproduction.

In this study, we observed that living *A. aomoriensis* was frequent in muddy sediments at the middle station FF1 of Flensburg Fjord during the entire period of investigation. Only in October 2009, *A. aomoriensis* was dominant in muddy sands at the outer Fjord station FF5. This occurrence peak was possibly related to a favourable calcite saturation state at this location in October. Furthermore, oxygen and nutrient input could also favour an increase in population densities of *A. aomoriensis* (Polovodova et al., 2009). Also at the middle Fjord station FF1, the population density of *A. aomoriensis* varied apparently during the seasonal cycle. On the other hand, station FF4 in southern Gelting Bay showed a noticeable low population density of *A. aomoriensis*. This part of Flensburg Fjord was reported as a quiet area with low mixing events in the water column (Exon, 1971). Therefore, seasonal stratification and respiration in the deeper water causes hypoxic zones and carbonate undersaturation, which could influence the survival and calcification of *A. aomoriensis*. The oxygen depletion could also promote the low *Ammonia* population densities at station FF4 (Alve and Nagy, 1986; Buzas-Stephens and Buzas, 2005; Polovodova and Schönfeld, 2008), even though sufficient food is available.

The low-oxic conditions would also explain the dominance of *E. incertum* living in the uppermost sediment layer during the whole year at station FF4. *Elphidium incertum* has been described as an intermediate-infaunal species, which dwells in the sediment down to 3–6 cm depth (Linke and Lutze, 1993). Under unfavorable oxygen conditions, this species moves into the uppermost sediment layers (Wefer, 1976). In the current study, living *E. incertum* showed irregular spatial and temporal fluctuations in Flensburg Fjord. Higher population densities of *E. incertum* were observed in the middle Fjord station FF1 in June and in the outer Fjord

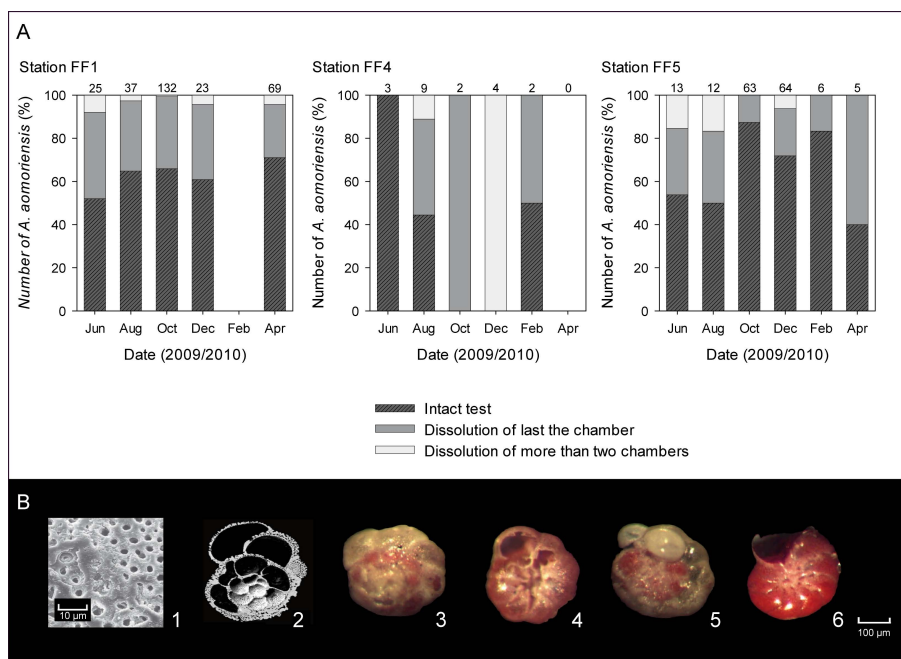


Fig. 7. (A): Three stages of preservation of living *A. aomoriensis*: intact tests, dissolution of the last chamber and dissolution of more than two chambers. Bars indicate the percentage of total species number of *A. aomoriensis* (Table 5) from June 2009 to April 2010. The number of counted *A. aomoriensis* specimens is present above each bar. **(B):** Subjacent SEM (1), EPMA (2) and light micrographs (3–6) of *A. aomoriensis* and *E. incertum* tests from Flensburg Fjord from Station FF5 in June 2009. 1–5 *A. aomoriensis*: detailed view of irregular test shape (1), spiral (2, 3 and 5) and umbilical (4) views of recalcifying (2 and 3) and dissolved tests (4 and 5). 6 spiral view of *E. incertum* with intact test, last chamber was broken.

station FF5 in April. The southern station FF4 in Gelting Bay, however, showed highest population densities of *E. incertum* in June and in April. Previous studies described that the reproduction of *E. incertum* preferentially takes place after phytoplankton blooms, which deliver high amounts of suspended organic particles to the sediment surface (Altenbach, 1985; Gustafsson and Nordberg, 1999). Indeed, we observed a dense layer of filamentous algae covering the sediment surface at all stations in June 2009. This algal mat probably induced and sustained the dense population of *E. incertum* in June, whereas the high and even rising population density in April was caused by the late spring diatom bloom in 2010 (Smetacek, 1985; Schönfeld and Numberger, 2007b).

The arenaceous species *A. cassis* was only common in the central and open parts of the outer Flensburg Fjord, where muddy sand prevailed. A higher number of living *A. cassis* was observed in October and December at station FF4. This transient peak correlated with the highest salinity values of 22.3 and 24.1 recorded at this station. It has been detected that the ability of *A. cassis* to live in the SW Baltic Sea is controlled by salinity (Lutze, 1965). A rising salinity due to decadal, massive saltwater inflows from the Kattegat had led to increasing abundances of *A. cassis* in Kiel Bight during the following years (Schönfeld and Numberger, 2007a; Nikulina et al., 2008). A further important process, which influenced the reproduction of *A. cassis* was the availability of

food particles, in particular their enrichment at hydrographic boundary layers and at the sediment surface bathed by these internal nepheloid layers (Wefer, 1976; Olsson, 1976). Given these favorable conditions, *A. cassis* bloomed and dominated the foraminiferal assemblages in August at station FF5.

5.3 Comparison with earlier findings

Polovodova et al. (2009) took sediment samples in June 2006 and described the recent living foraminiferal distribution in Flensburg Fjord. Three of the sampling stations were adjacent to our stations in June 2009. The comparison of both data sets revealed changes in living faunal composition within three years (Fig. 8).

Station PF16-19 of Polovodova et al. (2009) was closely located to our station FF1. Both stations showed a similar species composition, 18 % *A. aomoriensis* and 57 % *E. incertum* in June 2006 and 15 and 52 % in June 2009, respectively (Fig. 8). This similar species proportions revealed that the environmental setting did not change substantially between 2006 and 2009 at station FF1 in the middle Fjord.

Polovodova et al. (2009) stations PF-16-21 and PF-16-26 are close to our outer Fjord stations FF4 and FF5. From June 2006 to 2009, stations PF-16-21 and FF4, and PF-16-26 and FF5 showed a distinct faunal change. Living *A. aomoriensis* was dominant with 70 % (station PF-16-21) and

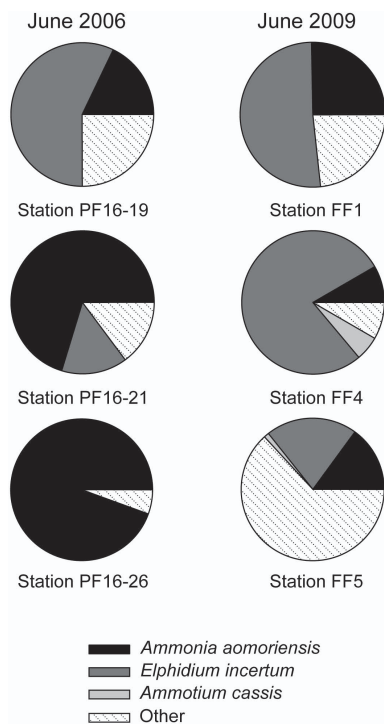


Fig. 8. Comparison of living benthic assemblages between the years 2006 and 2009.

94 % (station PF-16-26), whereas in 2009 living *E. incertum* dominated with 78 % at station FF4 and was common at FF5 with 21 % (Fig. 8). Furthermore, a small population of *A. cassisi* was observed before June 2009. This species comprised 6 % at station FF4 and 1 % at FF5.

On the one hand, this faunal change could reflect the year-to-year variability in parameters like salinity, food supply and oxygen content. The relationship with these parameters was documented for *A. beccarii*, *E. incertum* and *A. cassisi* in previous studies (Wefer, 1976; Polovodova et al., 2009).

On the other hand, it is known that benthic foraminifera reveal irregular distribution pattern on the sea floor (Ellison et al., 1986; Schafer, 1973). The degree of patchiness varies, for instance a clumped distribution of many species reflects reproduction events (Buzas, 1968). Patchy colonisation is a combination of many factors such as sediment composition (Bernstein et al., 1978; Bernstein and Meador, 1979) or microhabitat specialisation (Jumars, 1975). Patchiness of foraminiferal assemblages might play a certain role in the observed differences between the years and stations.

5.4 Response of living calcareous foraminifera to undersaturated Ω_{calc}

It is expected that foraminifera will respond negatively to ocean acidification (Cigliano et al., 2010; Haynert et al., 2011). Some laboratory studies revealed hampered calcification and decreased survival at elevated $p\text{CO}_2$ (Le Cadre

et al., 2003; Kuroyanagi et al., 2009; Allison et al., 2010; Haynert et al., 2011; Fujita et al., 2011), whereas other studies showed no significant change of calcification under simulated future $p\text{CO}_2$ scenarios (Dissard et al., 2010; McIntyre-Wressnig et al., 2011).

Population density of living *A. aomoriensis*, one of the dominating calcifying species, co-varies with sediment pore water undersaturation of Ω_{calc} . This finding is in agreement with observations from the laboratory, where mean test diameter of *A. aomoriensis* decreases in treatments with $\Omega_{\text{calc}} < 1$, by up to 22 % (Haynert et al., 2011).

In contrast, the fitness and survival of the symbiont-bearing benthic foraminifera *Amphistegina gibbosa* and *Archaias angulatus* were not directly affected by elevated $p\text{CO}_2$ up to 2000 μatm (McIntyre-Wressnig et al., 2011). But it is important to note that during the whole six week incubation time, Ω_{calc} was supersaturated ranging from 5.4 to 1.5. These results confirm our conclusion that living foraminifera are adapted to high $p\text{CO}_2$ levels, but respond most sensitive to an undersaturation of Ω_{calc} .

Furthermore, a previous study has been shown that *Ammonia tepida* revealed the highest calcification and survival rates at undersaturated conditions ($\Omega < 1$) (Dissard et al., 2010). These results emphasise the need to understand the biological control of the calcification process in different foraminiferal species.

To date, only a low number of field studies investigated the response of calcifying organisms in natural CO₂-rich habitats. At CO₂ vents off Ischia (Italy), settlement and overall abundance and species richness of benthic foraminifera was significantly decreased at the low pH (7.08) site, which was undersaturated with respect to calcite ($\Omega_{\text{calc}} = 0.75$) (Cigliano et al., 2010). In contrast, the current study exhibited that calcareous benthic foraminifera from Flensburg are able to survive and continue calcification under high $p\text{CO}_2$ and low pH values throughout the year. This infers no relationship between high $p\text{CO}_2$ -levels and the calcification process itself.

Differences between Flensburg Fjord and Ischia might be explained by higher, slightly supersaturated Ω_{calc} values in the sediment of Flensburg Fjord. In contrast, high $p\text{CO}_2$ cause undersaturated conditions in the open seawater at Ischia. Nevertheless, the saturation state itself, neither $p\text{CO}_2$ nor pH, seems to be the parameter which has an intense effect on calcification and test integrity of benthic foraminifera. Therefore, it needs to be considered that foraminifera may not be subjected to undersaturation within sediments, which might cause a much lower vulnerability to increased atmospheric $p\text{CO}_2$ as observed in the Ischia study (Cigliano et al., 2010).

5.5 Test dissolution

Biogenic calcification is expected to be highly affected by ocean acidification. Our study in Flensburg Fjord revealed no general impairment of calcification of living benthic

foraminifera in a naturally CO₂-rich coastal environment. Only in undersaturated water dissolution features were observed, but the response was clearly species specific. For instance, *E. incertum* did not exhibit any signs of dissolution, whereas *A. aomoriensis* showed several stages of test corrosion.

Similar dissolution features were observed in marginal marine foraminifera from several settings: Sandebukta, Nueces Bay, Flensburg Fjord and Cleveland Bay (Alve and Nagy, 1986; Buzas-Stephens and Buzas, 2005; Polovodova and Schönfeld, 2008), and on estuarine foraminifera from South Alligator River (Wang and Chappell, 2001). All these dissolution phenomena may have different background reasons inferred by anthropogenic or natural conditions (Le Cadre et al., 2003). Abrasion and predation were suggested by different authors as forces, which may act independently or amplify the foraminiferal shell loss (Bradshaw, 1957; Martin et al., 1995; Alve and Murray, 1999; Polovodova and Schönfeld, 2008). However, we observed similar stages of dissolution in a previous laboratory study with manipulated carbonate system. The experiment results supported our hypothesis of calcite undersaturation as the major reason for dissolution of *A. aomoriensis* tests, also in Flensburg Fjord (Haynert et al., 2011).

In Flensburg Fjord, we observed recalcification structures on tests of *A. aomoriensis*, which are explained by seasonal fluctuations of Ω_{calc} in the sediment pore water. After periods of $\Omega_{\text{calc}} < 1$, *A. aomoriensis* are seemingly able to rebuild their shell when Ω_{calc} returns to a supersaturated state > 1 . The same has been observed on tests of *Ammonia beccarii*, which begin to recalcify when pH was increased after a period of low pH levels (Le Cadre et al., 2003). The recalcification begins between the septal walls or around protruding cytoplasmic masses. Such a “repair” commonly leads to development of morphological abnormalities (Stouff et al., 1999; Le Cadre et al., 2000). Abnormal tests of foraminifera were also observed in Rio Una (Brazil), resulting from natural periodical acidification (Geslin et al., 2002).

In order to investigate, whether dissolution and recalcification had an influence on the growth of the specimens during their entire lifespan, we measured the size distribution in a specimen of *A. aomoriensis*. The diameter of living and dead *A. aomoriensis* ranged in average from 306 μm in minimum up to a maximum of 461 μm . Mean diameter of the dead assemblage ranged from 269 μm in minimum up to a maximum of 433 μm . The sizes of *A. aomoriensis* are in good general agreement with populations from North Sea tidal flats (Hazeleger, 2010) in Quarternary sediments from the Dead Sea Rift, Israel (Almogi-Labin et al., 1995). Size distribution histograms differ between the successive sampling dates. Large proportions of small-sized tests or single modes usually indicate reproduction events (Swallow, 2000). In Flensburg Fjord, increase in size from one sampling event to another was not recognised. This can be regarded as corroborating evidence for generation times shorter

than 88 days as reported by Bradshaw (1957, 1961). This infers that every *A. aomoriensis* population has to be regarded individually in the context of the environmental factors prevailing at the particular station about a couple of weeks before sampling. Therefore, certain foraminiferal species seem to cope much better with undersaturated conditions than others, which may eventually lead to future shifts in community structure.

Test dissolution in foraminifera is also known from the geological record (Alve, 1995, 1999). *Elphidium incertum* showed a higher resistance to undersaturation of Ω_{calc} in comparison to *A. aomoriensis*. Therefore, *A. aomoriensis* would be the better proxy for ocean acidification in the past. According to our results, calcification and recalcification of *A. aomoriensis* is a response to the environmental stress induced by changes in Ω_{calc} . High proportions of corroded tests of *A. aomoriensis* in sediment cores could indicate variations in ecological parameters, in particular elevated environmental stress. Therefore both, morphological abnormalities as well as dissolution features, might be useful proxies in paleoenvironmental reconstructions (Geslin et al., 2002).

5.6 Impact of rising atmospheric CO₂ on the carbonate chemistry of a coastal habitat

Future ocean acidification will amplify $p\text{CO}_2$ levels, especially in hypoxic water masses (Brewer and Pelzer, 2009; Melzner et al., 2012). Already today, low $[\text{CO}_3^{2-}]$ are encountered in the habitat of Flensburg Fjord. Additional CO₂ will cause further increases of seawater $p\text{CO}_2$ and lowering of $[\text{CO}_3^{2-}]$ (Melzner et al., 2012). According to our calculations, increasing CO₂ levels will also cause a strong increase of sediment pore water (0–1 cm) $p\text{CO}_2$ by about 1500 μatm to mean values of $3550 \pm 780 \mu\text{atm}$ (Fig. 9). At the same time, pH and Ω_{calc} will decrease to mean values of 7.42 ± 0.08 and 0.59 ± 0.20 (Fig. 9). This would lead to a constant undersaturation of sediment pore water Ω_{calc} during the whole year cycle (Fig. 9).

In consequence of increasing atmospheric CO₂ concentrations, a much higher $p\text{CO}_2$ increase is expected for seasonal hypoxic habitats such as Flensburg Fjord, in comparison to open ocean environments. Elevated $p\text{CO}_2$ or low pH may have not led to any drastic change of the benthic foraminiferal community structure yet. However, it is no doubt that certain species, in particular *A. aomoriensis*, have already exhibited high sensitivity to undersaturated states of present-day environment. In the future, more adverse conditions may lead to a strong decline in *A. aomoriensis* population density.

More tolerant calcareous species, such as *E. incertum*, may potentially dominate the benthic foraminiferal communities under future elevated $p\text{CO}_2$ conditions. This shift will eventually lead to changes in the benthic foraminiferal communities of Flensburg Fjord. The same will probably apply to

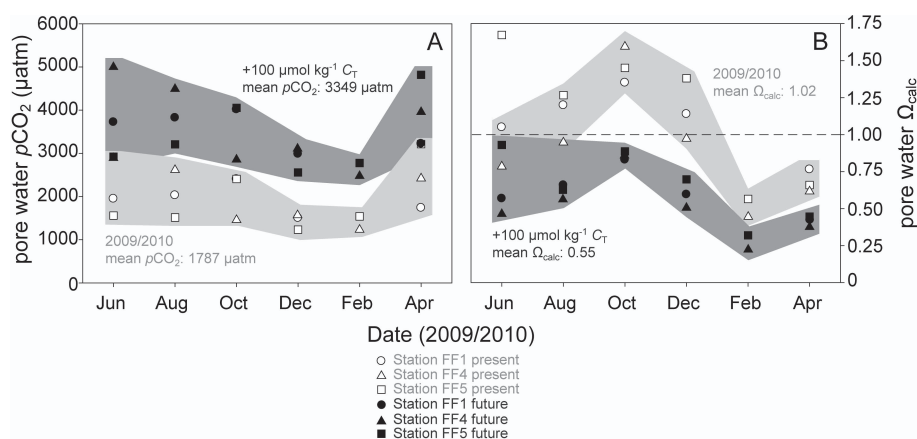


Fig. 9. Present (white symbols) and future (black symbols) sediment pore water (0–1 cm) $p\text{CO}_2$ (A) and Ω_{calc} (B) at stations FF1, FF4, and FF5. Future sediment pore water $p\text{CO}_2$ and Ω_{calc} were replotted from Table 4 and calculated after addition of $100 \mu\text{mol kg}^{-1} C_T$ to C_T from Table 4.

other regions too, which are going to experience naturally undersaturated Ω_{calc} levels.

Furthermore, planktonic foraminifers also precipitate thinner test walls at reduced carbonate ion concentrations and higher atmospheric CO₂ levels (Spero et al. 1997; Bijma et al., 1999; Moy et al., 2009; Manno et al., 2012). Therefore, calcareous planktonic foraminifera in the water column may be more affected by the future $p\text{CO}_2$ increase in comparison to benthic foraminifera living in the surface sediments. The reduction of calcification of planktonic foraminifera may have a considerable impact on global carbonate production. At present, planktonic foraminifera export 2.9 Gt CaCO₃ per year from the photic zone on a global scale (Schiebel, 2002), whereas calcareous benthic foraminifera in neritic environments produce 0.1 Gt yr^{-1} (Table S3 in the Supplement). This rate is about a magnitude lower than pelagic carbonate production. However, facing a future reduction in the export production of planktonic foraminifera, we may expect a relative increase of shallow-water benthic foraminiferal carbonate precipitation and thus a shift from pelagic to neritic carbonate production.

6 Conclusions

The present study is based on monitoring of the benthic foraminiferal assemblages in a naturally CO₂-rich coastal habitat of Flensburg Fjord. Bottom and sediment pore water $p\text{CO}_2$ showed large seasonal fluctuations and sediment pore water $p\text{CO}_2$ was constantly high during the entire year. Nevertheless, as a consequence of higher alkalinity (A_T), the sediment pore water was often supersaturated with respect to calcite. These observations indicate that the benthic community was subjected to high $p\text{CO}_2$.

The living and dead foraminiferal assemblages fluctuated seasonally but showed no direct relationship with sediment

pore water $p\text{CO}_2$, respectively Ω_{calc} . Instead, the population density of the living fauna showed fluctuations which can be attributed to the seasonality of food supply and organic matter degradation.

The population density of *A. aomoriensis*, one of the dominant calcifying species, co-varies with sediment pore water undersaturation of Ω_{calc} . In contrast, the co-occurring calcareous species *E. incertum* shows no relationship to $\Omega < 1$. Also the dissolution response of the foraminiferal tests differs between the two species. Whereas *E. incertum* displays no signs of test dissolution, *A. aomoriensis* shows different stages of test dissolution. Test dissolution of *A. aomoriensis* could indicate environmental stress, such as undersaturation of Ω_{calc} . Therefore, dissolution features offer useful proxies for paleoenvironmental reconstructions.

The calculated future sediment pore water acidification in Flensburg Fjord is much higher than expected for the global ocean. We conclude that benthic foraminifera are relatively tolerant to current high $p\text{CO}_2$ conditions in Flensburg Fjord, which suggest that elevated $p\text{CO}_2$ -levels do not lead to a drastic change in the foraminiferal communities. The modeled, future change of sediment pore water chemistry towards low, undersaturated Ω_{calc} , however, might increase the mortality of the dominating species *A. aomoriensis*, which will ultimately lead to changes in benthic foraminiferal communities for Flensburg Fjord.

Supplementary material related to this article is available online at: <http://www.biogeosciences.net/9/4421/2012/bg-9-4421-2012-supplement.pdf>.

Acknowledgements. The authors are grateful to the crew of R/V *Littorina* for help with sampling. We acknowledge Sebastian Fessler (GEOMAR) and Arne Körtzinger (GEOMAR) for supporting the carbonate system measurements, Ute Schuldt (Institute of Geosciences, Kiel) and Mario Thöner (GEOMAR) for technical support on the scanning electronic microscope. We also wish to thank Anna Nikulina (GEOMAR), who provided a map of the study area of Flensburg Fjord (SW Baltic Sea). We gratefully acknowledge the encouragement and advice of Frank Melzner (GEOMAR). The advice of two anonymous reviewers is gratefully acknowledged. This study was funded by the Excellence Cluster “Future Ocean” of Kiel University (grant no. CP 0801) and by the German Research Foundation (grant SCHO 605/7-1).

The service charges for this open access publication have been covered by a Research Centre of the Helmholtz Association.

Edited by: T. Treude

References

- Allison, N., Austin, W., Paterson, D., and Austin, H.: Culture studies of the benthic foraminifera *Elphidium williamsoni*: Evaluating pH, $\Delta[\text{CO}_3^{2-}]$ and inter-individual effects on test Mg/Ca, *Chem. Geol.*, 274, 87–93, 2010.
- Almogi-Labin, A., Siman-Tov, R., Rosenfeld, A., and Debard, E.: Occurrence and distribution of the foraminifer & *Ammonia beccarii tepida* (Cushman) in water bodies, Recent and Quaternary, of the Dead Sea Rift, Israel, *Mar. Micropaleontol.*, 26, 153–159, 1995.
- Altenbach, A. V.: Die Biomasse der benthischen Foraminiferen, Auswertungen von “Meteor”-Expeditionen im östlichen Nordatlantik, PhD-Thesis, CAU-Kiel, p. 167, 1985.
- Altenbach, A. V., Pflaumann, U., Schiebel, R., Thies, A., Timm, S., and Trauth, M.: Scaling percentages and distributional patterns of benthic Foraminifera with flux rates of organic carbon, *J. Foramin. Res.*, 29, 173–185, 1999.
- Alve, E.: Benthic foraminiferal distribution and recolonization of formerly anoxic environments in Drammensfjord, southern Norway, *Mar. Micropaleontol.*, 25, 169–186, 1995.
- Alve, E.: Colonization of new habitats by benthic foraminifera: a review, *Earth-Sci. Rev.*, 46, 167–185, 1999.
- Alve, E. and Murray, J. W.: Marginal marine environments of the Skagerrak and Kattegat: a baseline study of living (stained) benthic foraminifera, *Palaeogeogr. Palaeoclimatol.*, 146, 171–193, 1999.
- Alve, E. and Nagy, J.: Estuarine foraminiferal distribution in Sandebukta, a branch of the Oslo Fjord, *J. Foramin. Res.*, 16, 261–284, 1986.
- Archer, D.: Fate of fossil fuel CO₂ in geologic time, *J. Geophys. Res.*, 110, C09S05, doi:10.1029/2004JC002625, 2005.
- Asmus, R., Jensen, M. H., Murphy, D., and Doerffer, R.: Primary production of microphytobenthos, phytoplankton, and the annual yield of macrophytic biomass in the Sylt Rømø Wadden Sea, in: *Ökosystem Wattenmeer: Austausch, Transport und Stoffwandlungsprozesse*, edited by: Gätje, C. and Reise, K., Springer, Berlin, 367–391, 1998a.
- Asmus, H., Lackschewitz, D., Asmus, R., Scheiffarth, G., Nehls, G., and Herrmann, J. P.: Carbon flow in the food web of tidal flats in the Sylt–Rømø Bight, in: *Ökosystem Wattenmeer: Austausch, Transport und Stoffwandlungsprozesse*, edited by: Gätje, C. and Reise, K., Springer, Berlin, 393–420, 1998b.
- Bernstein, B. B. and Meador, J. P.: Temporal persistence of biological patch structure in an abyssal benthic community, *Mar. Biol.*, 51, 179–183, doi:10.1007/BF00555197, 1979.
- Bernstein, B. B., Hessler, R. R., Smith, R., and Jumars, P. A.: Spatial dispersion of benthic Foraminifera in the abyssal central North Pacific, *Limnol. Oceanogr.*, 23, 401–416, 1978.
- Bijma, J., Spero, H. J., and Lea, D. W.: Reassessing foraminiferal stable isotope geochemistry: impact of the oceanic carbonate system (experimental results), in: *Use of proxies in paleoceanography: examples from the South Atlantic*, edited by: Fisher, G. and Wefer, G., Springer, Heidelberg, 489–512, 1999.
- Borges, A. V. and Frankignoulle, M.: Daily and seasonal variations of the partial pressure of CO₂ in surface seawater along Belgian and southern Dutch coastal areas, *J. Mar. Syst.*, 19, 251–266, 1999.
- Borges, A. V. and Gypens, N.: Carbonate chemistry in the coastal zone responds more strongly to eutrophication than ocean acidification, *Limnol. Oceanogr.*, 55, 346–353, 2010.
- Borges, A. V., Schiettecatte, L. S., Abril, G., Delille, B., and Gazeau, F.: Carbon dioxide in European coastal waters, *Estuar. Coast. Shelf S.*, 70, 375–387, 2006.
- Bradshaw, J.: Laboratory studies on the rate of growth of the foraminifer *Streblus beccarii* (Linne) var. *tepidus* (Cushman), *J. Paleontol.*, 31, 1138–1147, 1957.
- Bradshaw, J.: Laboratory experiments on the ecology of foraminifera, *Contrib. Cushman Found. J. Foramin. Res.*, 7, 95–107, 1961.
- Brewer, P. G. and Peltzer, E. T.: Limits to marine life, *Science*, 324, 347–348, 2009.
- Buzas, M. A.: On the spatial distribution of foraminifera, *Contrib. Cushman Found. J. Foramin. Res.*, 19, 411–422, 1968.
- Buzas-Stephens, P. and Buzas, M. A.: Population dynamics and dissolution of Foraminifera in Nueces Bay, Texas, *J. Foramin. Res.*, 35, 248–258, 2005.
- Caldeira, K. and Wickett, M. E.: Ocean model predictions of chemistry changes from carbon dioxide emissions to the atmosphere and ocean, *J. Geophys. Res.*, 110, C09S04, doi:10.1029/2004JC002671, 2005.
- Cigliano, M., Gambi, M. C., Rodolfo-Metalpa, R., Patti, F. P., and Hall-Spencer, J. M.: Effects of ocean acidification on invertebrate settlement at volcanic CO₂ vents, *Mar. Biol.*, 157, 2489–2502, doi:10.1007/s00227-010-1513-6, 2010.
- Conley, D. J., Björck, S., Bonsdorff, E., Carstensen, J., Destouni, G., Gustafsson, B. G., Hietanen, S., Kortekaas, M., Kuosa, H., Meier, M. H. E., Müller-Karulis, B., Nordeberg, K., Norkko, A., Nürnberg, G., Pitkänen, H., Rabalais, N. N., Rosenberg, R., Savchuck, O. P., Slomp, C. P., Voss, M., Wulff, F., and Zillen, L.: Hypoxia-related processes in the Baltic Sea, *Environ. Sci. Technol.*, 43, 3412–3420, 2009.
- Diaz, R. J. and Rosenberg, R.: Spreading dead zones and consequences for marine ecosystems, *Science*, 321, 926–929, 2008.

- Dickson, A. G.: Standard potential of the reaction $\text{AgCl}_s + 1/2 \text{H}_2 = \text{Ag}_s + \text{HCl}_{\text{aq}}$ and the standard acidity constant of the ion HSO_4^- in synthetic sea-water from 273.15-K to 318.15-K, *J. Chem. Thermodyn.*, 22, 113–127, 1990.
- Dickson, A. G. and Millero, F. J.: A comparison of the equilibrium constants for the dissociation of carbonic acid in seawater media, *Deep-Sea Res.*, 34, 1733–1743, 1987.
- Dickson, A. G., Afghan, J. D., and Anderson, G. C.: Reference materials for oceanic CO₂ analysis: a method for the certification of total alkalinity, *Mar. Chem.*, 80, 185–197, 2003.
- Dickson, A. G., Sabine, C. L., and Christian, J. R.: Guide to best Practices for Ocean CO₂ Measurements, PICES Special Publications, PICES, Sidney, 191 pp., 2007.
- Dissard, D., Nehrke, G., Reichert, G. J., and Bijma, J.: Impact of seawater pCO₂ on calcification and Mg/Ca and Sr/Ca ratios in benthic foraminifera calcite: results from culturing experiments with *Ammonia tepida*, *Biogeosciences*, 7, 81–93, doi:10.5194/bg-7-81-2010, 2010.
- Ellison, R., Broome, R., and Ogilvie, R.: Foraminiferal response to trace metal contamination in the Patapsco River and Baltimore Harbour, Maryland, *Mar. Pollut. Bull.*, 17, 419–423, 1986.
- Erez, J.: The source of ions for biomineralization in foraminifera and their implications for paleoceanographic proxies, *Rev. Mineral. Geochem.*, 54, 115–149, 2003.
- Exon, N.: Holocene sedimentation in and near the outer Flensburg Fjord (westernmost Baltic Sea), PhD-thesis, CAU Kiel, p. 102, 1971.
- Exon, N.: Sedimentation in the outer Flensburg Fjord area (Baltic Sea) since the last Glaciation, *Meyniana*, 22, 5–6, 1972.
- Fabricius, K. E., Langdon, C., Uthicke, S., Humphrey, C., Noonan, S., De'ath, G., Okazaki, R., Muehlehner, N., Glas, M. S., and Lough, J. M.: Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations, *Nature Clim.*, 1, 165–169, 2011.
- Feely, R. A., Sabine, C. L., Lee, K., Berelson, W., Kleypas, J., Fabry, V. J., and Millero, F. J.: Impact of anthropogenic CO₂ on the CaCO₃ system in the oceans, *Science*, 305, 362–366, 2004.
- Frenzel, P., Tech, T., and Bartholdy, J.: Checklist and annotated bibliography of Recent Foraminifera from the German Baltic Sea coast, in: *Methods and applications in micropaleontology*, edited by: Tyszka, J., *Stud. Geol. Pol.*, 124, 67–86, 2005.
- Fujita, K., Hikami, M., Suzuki, A., Kuroyanagi, A., Sakai, K., Kawahata, H., and Nojiri, Y.: Effects of ocean acidification on calcification of symbiont-bearing reef foraminifera, *Biogeosciences*, 8, 2089–2098, doi:10.5194/bg-8-2089-2011, 2011.
- Gattuso, J.-P., Frankignoulle, M., Bourge, I., Romaine, S., and Buddemeier, R. W.: Effect of calcium carbonate saturation of seawater in coral calcification, *Global Planet. Change*, 18, 37–46, 1998.
- Geslin, E., Debenay, J. P., Duleba, W., and Bonetti, C.: Morphological abnormalities of foraminiferal tests in Brazilian environments: comparison between polluted and nonpolluted areas, *Mar. Micropaleontol.*, 45, 151–168, 2002.
- Gooday, A. J.: Benthic foraminifera (protista) as tools in deep-water palaeoceanography: Environmental influences on faunal characteristics, *Mar. Biol.*, 46, 1–90, 2003.
- Grobe, H. and Fütterer, D.: Zur Fragmentierung benthischer Foraminiferen in der Kieler Bucht (Westliche Ostsee), *Meyniana*, 33, 85–96, 1981.
- Gustafsson, M. and Nordberg, K.: Benthic foraminifera and their response to hydrography, periodic hypoxic conditions and primary production in the Koljö fjord on the Swedish west coast, *J. Sea Res.*, 41, 163–178, 1999.
- Hall-Spencer, J. M., Rodolfo-Metalpa, R., Martin, S., Ransome, E., Fine, M., Turner, S. M., Rowley, S. J., Tedesco, D., and Buia, M.-C.: Volcanic carbon dioxide vents show ecosystem effects of ocean acidification, *Nature*, 454, 96–99, 2008.
- Haynert, K., Schönfeld, J., Riebesell, U., and Polovodova, I.: Biometry and dissolution features of the benthic foraminifer *Ammonia aomoriensis* at high pCO₂, *Mar. Ecol. Prog. Ser.*, 432, 53–67, 2011.
- Hazeleger, J. H.: In situ foraminifera food dynamics on an intertidal mudflat after a severe induced hypoxia Western Scheldt, Netherlands, Faculty of Geosciences Theses, University Utrecht, 2010.
- Hofmann, G. E., Smith, J. E., Johnson, K. S., Send, U., Levin, L. A., Micheli, F., Paytan, A., Price, N. N., Peterson, B., Takeshita, Y., Matson, P. G., Crook, E. D., Kroeker, K. J., Gambi, M. C., Rivest, E. B., Frieder, C. A., Yu, P. C., and Martz, T. R.: High-frequency dynamics of ocean pH: a multi-ecosystem comparison, *PLOS ONE*, 6, e28983, doi:10.1371/journal.pone.0028983, 2011.
- Ivanenkov, V. N. and Lyakhin, Y. I.: Determination of total alkalinity in seawater, in: *Methods of Hydrochemical Investigations in the Ocean*, edited by: Borodovsky, O. K. and Ivanenkov, V. N., Nauka, Moscow, 110–114, 1978.
- Jumars, P. A.: Environmental grain and polychaete species' diversity in a bathyal benthic community, *Mar. Biol.*, 30, 253–266, 1975.
- Kleypas, J. A., Buddemeier, R. W., Archer, D., Gattuso, J. P., Langdon, C., and Opdyke, B. N.: Geochemical consequences of increased atmospheric CO₂ on coral reefs, *Science*, 284, 118–120, 1999.
- Kristensen, E., Jensen, M. H., and Jensen, K. M.: Sulfur dynamics in sediments of Königshafen, in: *Ökosystem Wattenmeer: Austausch, Transport und Stoffwandlungsprozesse*, edited by: Gätje, C. and Reise, K., Springer, Berlin, 233–256, 1998.
- Kuroyanagi, A., Kawahata, H., Suzuki, A., Fujita, K., and Irie, T.: Impacts of ocean acidification on large benthic foraminifera: results from laboratory experiments, *Mar. Micropaleontol.*, 73, 190–195, 2009.
- Le Cadre, V., Debenay, J. P., and Lesourd, M.: Low pH effects on test deformation: implications for studying test deformations as a pollution indicator, in: *The Second International Conference on Application of Micro- and Microorganisms to Environmental Problems*, Winnipeg, Canada, p. 74, 2000.
- Le Cadre, V., Debenay, J. P., and Lesourd, M.: Low pH effects on *Ammonia beccarii* test deformation: implications for using test deformations as a pollution indicator, *J. Foramin. Res.*, 33, 1–9, 2003.
- Lewis, E. and Wallace, D. W. R.: Program developed for CO₂ system calculations, Oak Ridge, Oak Ridge National Laboratory ORNL/CDIAC, Oak Ridge, 105, 1998.
- Linke, P. and Lutze, G. F.: Microhabitat preferences of benthic foraminifera – a static concept or a dynamic adaptation to optimize food acquisition?, *Mar. Micropaleontol.*, 20, 215–234, 1993.

- Lutze, G. F.: Zur Foraminiferen-Fauna der Ostsee, *Meyniana*, 15, 75–142, 1965.
- Lutze, G. F.: Foraminiferen der Kieler Bucht (Westliche Ostsee): 1 “Hausgartengebiet” des Sondersforschungsbereiches 95 der Universität Kiel, *Meyniana*, 26, 9–22, 1974.
- Lutze, G. F. and Altenbach, A.: Technik und Signifikanz der Lebendfärbung benthischer Foraminiferen mit Bengalrot, *Geolog. Jahrbuch*, A128, 251–265, 1991.
- Manno, C., Morata, N., and Bellerby, R.: Effect of ocean acidification and temperature increase on the planktonic foraminifer *Neogloboquadrina pachyderma* (sinistral), *Polar Biol.*, 35, 1311–1319, doi:10.1007/s00300-012-1174-7, 2012.
- Martin, R. E., Harris, M. S., and Liddell, W. D.: Taphonomy and time-averaging of foraminiferal assemblages in Holocene tidal flat sediments, Bahia la Choya, Sonora, Mexico (northern Gulf of California), *Mar. Micropaleontol.*, 26, 187–206, 1995.
- McIntyre-Wressnig, A., Bernhard, J. M., McCorkle, D. C., and Hallock, P.: Non-lethal effects of ocean acidification on two symbiont-bearing benthic foraminiferal species, *Biogeosciences Discuss.*, 8, 9165–9200, doi:10.5194/bgd-8-9165-2011, 2011.
- Mehrbach, C., Culberso, C. H., Hawley, J. E., and Pytkowic, R. W.: Measurement of the apparent dissociation-constants of carbonic acid in seawater at atmospheric-pressure, *Limnol. Oceanogr.*, 18, 897–907, 1973.
- Melzner, F., Thomsen, J., Koeve, W., Oschlies, A., Gutowska, M. A., Bange, H. W., Hansen, H. P., and Körtzinger, A.: Future ocean acidification will be amplified by hypoxia in coastal habitats, *Mar. Biol.*, doi:10.1007/s00227-012-1954-1, in press, 2012.
- Mintrop, L., Perez, F. F., Gonzalez-Davila, M., Santana-Casiano, M. J., and Körtzinger, A.: Alkalinity determination by potentiometry: Intercalibration using three different methods, *Cienc. Mar.*, 26, 23–37, 2000.
- Morigi, C., Jorissen, F. J., Gervais, A., Guichard, S., and Borsetti, A. M.: Benthic foraminiferal faunas in surface sediments off NW Africa: relationship with the organic flux to the ocean floor, *J. Foramin. Res.*, 31, 350–368, 2001.
- Moy, A. D., Howard, W. R., Bray, S. G., and Trull, T. W.: Reduced calcification in modern Southern Ocean planktonic foraminifera, *Nat. Geosci.*, 2, 276–280, 2009.
- Nikulina, A. and Dullo, W. C.: Eutrophication and heavy metal pollution in the Flensburg Fjord: a reassessment after 30 years, *Mar. Pollut. Bull.*, 58, 905–915, 2009.
- Nikulina, A., Polovodova, I., and Schönfeld, J.: Foraminiferal response to environmental changes in Kiel Fjord, SW Baltic Sea, *Earth (Waukesha)*, 3, 37–49, 2008.
- Olsson, I.: Distribution and ecology of foraminiferan *Ammotium cassis* (Parker) in some Swedish estuaries, *Zoon*, 4, 137–147, 1976.
- Otto, G. H.: Comparative tests of several methods of sampling heavy mineral concentrates, *J. Sediment. Petrol.*, 3, 30–39, 1933.
- Polovodova, I. and Schönfeld, J.: Foraminiferal test abnormalities in the western Baltic Sea, *J. Foramin. Res.*, 38, 318–336, 2008.
- Polovodova, I., Nikulina, A., Schönfeld, J., and Dullo, W. C.: Recent benthic foraminifera in the Flensburg Fjord, *J. Micropaleontol.*, 28, 131–142, 2009.
- Provoost, P., van Heuven, S., Soetaert, K., Laane, R. W. P. M., and Middelburg, J. J.: Seasonal and long-term changes in pH in the Dutch coastal zone, *Biogeosciences*, 7, 3869–3878, doi:10.5194/bg-7-3869-2010, 2010.
- Raven, J., Caldeira, K., Elderfield, H., Hoegh-Guldberg, O., Liss, P., Riebesell, U., Shepherd, J., Turley, C., and Watson, A.: Ocean acidification due to increasing atmospheric carbon dioxide, The Royal Society policy document 12/05, The Clyvedon Press Ltd, Cardiff, 2005.
- Riebesell, U., Zondervan, I., Rost, B., Tortell, P. D., Richard, E. Z., and Morel, F. M. M.: Reduced calcification of marine plankton in response to increased atmospheric CO₂, *Nature*, 407, 364–367, 2000.
- Rottgardt, D.: Mikropaläontologische wichtige Bestandteile rezenter brackischer Sedimente an den Küsten Schleswig-Holsteins, *Meyniana*, 1, 169–228, 1952.
- Schafer, C. T.: Distribution of foraminifera near pollution sources in Chaleur Bay, *Water Air Soil Poll.*, 2, 219–233, 1973.
- Schiebel, R.: Planktic foraminiferal sedimentation and the marine calcite budget, *Global Biogeochem. Cy.*, 16, 1065, doi:10.1029/2001GB001459, 2002.
- Schönfeld, J. and Numberger, L.: Seasonal dynamics and decadal changes of benthic foraminiferal assemblages in the western Baltic (NW Europe), *J. Micropaleontol.*, 26, 47–60, 2007a.
- Schönfeld, J. and Numberger, L.: The benthic foraminiferal response to the 2004 spring bloom in the western Baltic Sea, *Mar. Micropaleontol.*, 65, 78–95, 2007b.
- Smetacek, V.: The annual cycle of Kiel Bight Plankton: a long-term analysis, *Estuaries*, 8, 145–157, 1985.
- Spero, H. J., Bijma, J., Lee, D. W., and Bemis, B. E.: Effect of seawater carbonate concentration on foraminiferal carbon and oxygen isotopes, *Nature*, 390, 497–500, 1997.
- Stouff, V., Geslin, E., Debenay, J. P., and Lesourd, M.: Origin of morphological abnormalities in *Ammonia* (Foraminifera): studies in laboratory and natural environments, *J. Foramin. Res.*, 29, 152–170, 1999.
- Swallow, J. E.: Intra-annual variability and patchiness in living assemblages of salt-marsh foraminifera from Mill Rythe Creek, Chichester Harbour, England, *J. Micropaleontol.*, 19, 9–22, 2000.
- Thomas, H., Schiettecatte, L.-S., Suykens, K., Koné, Y. J. M., Shadwick, E. H., Prowe, A. E. F., Bozec, Y., de Baar, H. J. W., and Borges, A. V.: Enhanced ocean carbon storage from anaerobic alkalinity generation in coastal sediments, *Biogeosciences*, 6, 267–274, doi:10.5194/bg-6-267-2009, 2009.
- Thomsen, J., Gutowska, M. A., Saphörster, J., Heinemann, A., Trübenbach, K., Fietzke, J., Hiebenthal, C., Eisenhauer, A., Körtzinger, A., Wahl, M., and Melzner, F.: Calcifying invertebrates succeed in a naturally CO₂-rich coastal habitat but are threatened by high levels of future acidification, *Biogeosciences*, 7, 3879–3891, doi:10.5194/bg-7-3879-2010, 2010.
- Wang, P. and Chappell, J.: Foraminifera as Holocene environmental indicators in the South Alligator River, northern Australia, *Quatern. Int.*, 83–85, 47–62, 2001.
- Wefer, G.: Umwelt, Produktion und Sedimentation benthischer Foraminiferen in der westlichen Ostsee, *Reports Sonderforschungsbereich 95 Wechselwirkung Meer-Meeresboden*, 14, 1–103, 1976.
- Yao, W. and Millero, F. J.: The Chemistry of the Anoxic Waters in the Framvaren Fjord, Norway, *Aquat. Geochem.*, 1, 53–88, 1995.
- Zeebe, R. E. and Wolf-Gladrow, D.: CO₂ in seawater: equilibrium, kinetics, isotopes, in: Elsevier oceanography series, Series 65, edited by: Halpern, D., Elsevier, Amsterdam, 2001.