Biogeosciences Discuss., 10, 9523–9572, 2013
www.biogeosciences-discuss.net/10/9523/2013/
doi:10.5194/bgd-10-9523-2013
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Biogeosciences Discussions
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Response of benthic foraminifera to ocean acidification in their natural sediment environment: a long-term culturing experiment

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Received: 13 May 2013 – Accepted: 27 May 2013 – Published: 13 June 2013

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Published by Copernicus Publications on behalf of the European Geosciences Union.

Abstract

Calcifying foraminifera are expected to be endangered by ocean acidification, However, the response of a complete community kept in natural sediment and over multiple generations under controlled laboratory conditions has not been constrained to date. During six month incubation, foraminiferal assemblages were treated with pCO_2 enriched seawater of 430, 907, 1865 and 3247 µatm pCO_2. The fauna was dominated by *Ammonia aomoriensis* and *Elphidium* species, whereas agglutinated species were rare. After 6 months incubation, pore water alkalinity was much higher in comparison to the overlying seawater. Consequently, the saturation state of Ω_{calc} was much higher in the sediment than in the water column in all pCO_2 treatments and remained close to saturation. As a result, the life cycle of living assemblages was largely unaffected by the tested pCO_2 treatments. Growth rates, reproduction and mortality, and therefore population densities and size-frequency distribution of *Ammonia aomoriensis* varied markedly during the experimental period. Growth rates varied between 25 and 50 µm per month, which corresponds to an addition of 1 or 2 new chambers per month. According to the size-frequency distribution, foraminifera start reproduction at a diameter of 250 µm. Mortality of large foraminifera was recognized, commencing at a test size of 285 µm at a pCO_2 ranging from 430 to 1865 µatm, and of 258 µm at 3247 µatm. The total organic content of living *Ammonia aomoriensis* has been determined to be 4.3 % of dry weight. Living individuals had a calcium carbonate production rate of 0.47 g m^{-2} yr^{-1}, whereas dead empty tests accumulated at a rate of 0.27 g $m^{-2}a^{-1}$. Although Ω_{calc} was close to 1, some empty tests of *Ammonia aomoriensis* showed dissolution features at the end of incubation. In contrast, tests of the subdominant species, *Elphidium incertum*, stayed intact. This species specific response could be explained by differences in the elemental test composition, in particular the higher Mg-concentrations in *Ammonia aomoriensis* tests. Our results emphasize that the sensitivity to ocean acidification of endobenthic foraminifera in their natural sediment habitat is much lower compared to the experimental response of specimens isolated from the sediment.

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1 Introduction

Benthic foraminifera are the most diverse group of hard-shelled protists. They live at the sediment–water interface, especially in the uppermost 0–1 cm, or within oxygenated sediments down to > 12 cm depth (Corliss, 1985). It is expected that calcifying foraminifera will be adversely affected by the ongoing acidification of the oceans. Surprisingly, previous experimental studies did not report a consistent and uniform response when living specimens were subjected to simulated ocean acidification. Most benthic foraminifera were negatively affected by high pCO_2 (Le Cadre et al., 2003; Kuroyanagi et al., 2009; Allison et al., 2010; Dissard et al., 2010; Fujita et al., 2011; Haynert et al., 2011; Uthicke et al., 2013). In contrast, some species showed an indistinct sensitivity under elevated pCO_2 (Vogel and Uthicke, 2012; McIntyre-Wressnig et al., 2013). Keul et al. (2013) revealed that not pCO_2, but rather CO_3^{2-} is the parameter which affects the test size and dry weights of *Ammonia* species. All these studies cultured living benthic foraminifera as isolated specimens without any natural sediment.

To date, no ocean acidification studies were reported to pursue culturing experiments with benthic foraminifera in their natural sedimentary environment. The field study of Haynert et al. (2012) in Flensburg Fjord exhibited that the carbonate chemistry of sediment pore water differed strongly from the conditions in the overlying near-bottom water. Sediment pore water pCO_2 was constantly high, ranging from 1244 to 3324 µatm during the entire year. Nevertheless, as a consequence of higher alkalinity, Ω_{calc} was slightly supersaturated. Under these conditions the benthic foraminiferal community was not affected by seasonally elevated bottom water pCO_2.

Benthic foraminifera are common in Kiel Fjord, western Baltic Sea, although seawater carbonate concentrations are permanently low and seasonally undersaturated with respect to Ω_{calc} (Thomsen et al., 2013). High biological activity and nutrient inputs characterize the area, and organic-rich mud prevails in Kiel Fjord (Nikulina et al., 2008). Degradation of organic matter between the sediment–water interface influences the underlying sediment chemistry (Graf et al., 1984), and therefore the habitat of benthic

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foraminifera. Benthic foraminifera in Kiel Fjord sediments were described in previous studies, initiated by Rhumbler (1935), followed by Rottgardt (1952), Lutze (1965), Wefer (1976), Nikulina et al. (2008) and Polovodova et al. (2008). These studies focused on taxonomy and distribution, and influences of temperature, salinity, oxygen, heavy metals and food supply, but did not consider possible impacts of seawater carbonate chemistry.

Kiel Fjord represents a suitable habitat, where benthic foraminifera were found with high population densities. The aim of this study was to investigate the response of foraminiferal population by using a pristine assemblage from Kiel Fjord to elevated pCO_2 in their natural sedimentary environment during a long-term incubation over six months.

2 Materials and methods

2.1 Field sampling and preparation

Foraminiferal samples were collected from station KF1 (54° 20′ 713″ N, 10° 10′ 160″ E, 13 m water depth) in Kiel Fjord, southwestern Baltic Sea, at the end of April 2011. At this location, the bottom sediment is silty fine sand. The sampling site was similar to a previous sampling station PF15-13 of Polovodova and Schönfeld (2008), where *Ammonia aomoriensis* (similar to *Ammonia beccarii* of Nikulina et al. (2008) and Polovodova et al., 2009) is one of the dominating species in the living assemblage.

Surface sediment samples were taken with a Mini Muc K/MT 410 corer equipped with four tubes of 60 cm length and 10 cm inner diameter (Kuhn and Dunker, 1994), deployed from R/V *Polarfuchs*. Altogether, 24 cores were taken. A graduated plastic ring was used to slice off the uppermost one centimeter of the surface sediment (Schönfeld et al., 2012). The surface layer was transferred with a spoon into 300 mL Kautex™ wide-neck containers. The samples were covered with bottom water taken from the supernatant water of the coring tubes. On board, the containers were covered

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with Parafilm to avoid contamination by dust or evaporation. Afterwards, the samples were immediately brought to the laboratory at GEOMAR, where they were acclimated to culturing conditions at 17 °C room temperature for four weeks. During that acclimation period, stock cultures were aerated with compressed, humidified air and fed with 200 µL DT's Premium Blend containing living algae of *Nannochloropsis oculata*, *Phaeodactylum tricornutum* and *Chlorella* once a week.

After four weeks of acclimation, the seawater of the stock cultures was sucked off except for a few millimeters above the sediment surface. The sediment was homogenized with a spoon for a few minutes. This technique was a simple and gentle way to achieve an even distribution pattern of benthic foraminifera inside the sediment. After homogenization, each culture vessel was filled with 0.4 cm of sediment by using a spoon-shaped plastic spatula. At the end of the experiment, the measured sediment height was 0.36 cm on average, which results at a given culture vessel area of 42.25 cm^2 in a mean sample volume of 15.2 cm^3. We prepared 84 culture vessels, three replicates for four pCO_2 lines (380, 1120, 2400 and 4000 µatm), combined seven replicate sets per pCO_2 treatment were terminated. After spreading of the sediment, the culture vessels were transferred into the experimental set up and filled up with seawater from Kiel Fjord. For acclimatization and in order to restore the natural pore water chemistry in the sediments, the culture vessels were kept for 20 days at temperature of 17 °C and a salinity of 16 until the start of the experiment. This time was deemed necessary to achieve a full recovery of foraminiferal microhabiat pattern in a sub-cm scale (Ernst et al., 2002). During that time, 400 µL DT's Premium Blend were added weekly into each culture vessel.

2.2 Experimental design

The culturing of benthic foraminiferal assemblages from Kiel Fjord was performed in a closed flow-through system modified after Hintz et al. (2004) and Haynert et al. (2011). The culture vessels (6.5 × 6.5 × 4.5 cm) with an area of 42.25 cm^2 were filled with a 0.4 ± 0.1 cm sediment layer and an overlying seawater column of 4 cm.

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A nepheloid detritus layer of 0.1 cm separated the seawater from the underlying sediment pore water. The resulting pore water stagnation equates the conditions in their natural habitat, where foraminifera concentrate in the upper oxic surface layer of the sediment (Haynert et al., 2012). During field sampling we observed that the oxic sediment layer varied between 0.5 and 0.8 cm.

Each culture vessel was flushed with 25 µm cartridge-filtered and UV-sterilized seawater from Kiel Fjord. Four pCO_2 levels were adjusted by aeration of 5 L compact jerrycans with compressed and CO_2 enriched air. The target pCO_2 levels were 380, 1120, 2400 and 4000 µatm. Treatment levels were chosen in order to simulate present day and future pCO_2 peaks, which are transiently occurring today and are going to prevail for longer periods in future in Kiel Fjord (Thomsen et al., 2010, 2013; Melzner et al., 2012). The preconditioned seawater from each tank flowed through the culture vessels, which were three times replicated for each pCO_2 level. The overflow seeped through the fissure between lid and vessel, and draining off to a sink. The flow rate was adjusted to 0.16 mL s^{-1}, which is sufficient to replace the water volume of the vessels 1.4 times per hour. The overflow drained off to a 60 L catchment tank. In the catchment tank, the water was sparged with compressed air at a high rate, in order to remove the excess CO_2 before the water was pumped back to the compact jerrycans. In order to avoid evaporation by aeration of the seawater with compressed and thus dry air, the gas was humidified in gas-washing bottles which were inserted in each compressed air connection. Evaporation of one liter per week was compensated by refilling the system with deionised water. Food (400 µL DT's Premium Blend) was added to each culture vessel every week.

Seawater temperature, salinity and pH_{NBS} (National Bureau of Standards pH-scale) were measured weekly in each culture vessel. Total dissolved inorganic carbon (C_T), phosphate (PO_4^{3-}) and silicate (Si) concentrations were determined monthly in one of the three replicates for each pCO_2-level. After six months, carbonate system parameters of total alkalinity (A_T) and pH_{NBS} of supernatant seawater and sediment pore water were measured in one of the three replicates per pCO_2-level.

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In order to monitor changes of the foraminiferal community during the incubation time, the sediment of three culture vessel replicates was analyzed monthly for foraminiferal assemblage composition. The experiment ended after six months.

2.3 Determination of water chemistry parameters

Seawater pH_{NBS}, temperature and salinity were determined with a WTW 340i pH analyzer and a WTW Cond 315i conductivity meter. The pH_{NBS}-electrode was calibrated with standard buffer solutions of pH 4.01, 7.00 and 10.00 (WTW standard, DIN/NIST buffers L7A). Precision was ±0.01 for pH_{NBS} and ±0.1 °C for temperature. The precision of the conductivity meter was ±0.1 salinity units. Nutrient concentrations were analyzed in sterile-filtered (0.2 µm pore size) water samples. Phosphate (PO_4^{3-}) and silicate (Si) were analyzed colorimetrically in a spectrophotometer (U 2000; Hitachi-Europe) at a wavelength of 882 nm and 810 nm according to Koroleff and Grasshof (1983). The measurement precision was ±0.2 µmol L^{-1} for phosphate and, in dependence of the concentrations, 2.5 to 6 % for silicate.

Total dissolved inorganic carbon (C_T) was analyzed in sterile-filtered (0.2 µm pore size) water samples taken from the culture vessels during the incubation time using an AIRICA autoanalyzer (Maranda GmbH, Kiel, Germany) with a precision of 2–4 µmol kg^{-1}. The accuracy of the C_T measurements was ensured by using certified reference material provided by Andrew Dickson of the Scripps Institution of Oceanography. Seawater carbonate system parameters pCO_2, total alkalinity (A_T) and omega for calcite (Ω_{calc}) were calculated from pH_{NBS}, C_T, temperature, salinity, PO_4^{3-} and Si values using CO2SYS software by Lewis and Wallace (1998). Dissociation constants K_1 and K_2 were chosen according to Mehrbach et al. (1973) as refitted by Dickson and Millero (1987) and $KHSO_4$ dissociation constant after Dickson (1990).

Water chemistry parameters of pH_{NBS}, A_T, temperature and salinity were analyzed from the seawater and sediment pore water of selected culture vessels. Seawater samples from 0–2 cm and 2–4 cm water layers were sterile-filtered (0.2 µm pore size) and transferred directly into 20 mL PVC bottles. For sediment pore water analyses,

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sediment samples were transferred into 50 mL centrifuge tubes and centrifuged at 3000 rpm for 15 min in order to separate the sediment pore water from the sediment. The extracted pore water was transferred through 0.2 µm sterile filters into 20 mL PVC bottles. pH_{NBS} and temperature were measured using the WTW 340i pH analyzer, salinity was determined with WTW Cond 315i conductivity meter. Total alkalinity (A_T) 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 0.02M HCl and finished until a stable light pink colour occurred. During titration, the sample was degassed by continuously bubbling argon through the solution in order to remove the generated CO_2 or H_2S. The measured values were standardized using an IAPSO seawater solution. The precision of the alkalinity measurements was 0.37 %. Carbonate parameters pCO_2, C_T and Ω_{calc} of seawater and sediment pore water were calculated from measured pH_{NBS}, A_T, temperature, salinity, PO_4^{3-} and Si values according to dissociation constants as specified above. All chemical parameters are reported as mean values of replicate measurements (Table 1).

2.4 Foraminiferal processing

Benthic foraminiferal sediment samples were transferred in 100 mL Kautex™ wide-neck containers, preserved and stained with Rose Bengal ethanol (94 %) solution of 2 g L^{-1} for three weeks following Lutze and Altenbach (1991). This period is sufficient to stain the protoplasm completely with Rose Bengal in all tests of foraminifera (Schönfeld et al., 2012).

Samples were first passed through a 2000 µm screen in order to remove mollusks shells and pebbles. Subsequently the samples were gently washed with tap water through a 63 µm sieve. The 63–2000 µm and > 2000 µm fractions were dried at 60 °C for at least 24 h. The size fraction 63–2000 µm was picked completely for living and dead foraminifera. Samples were not split. All Rose Bengal stained foraminifera were considered as living at the time of sampling, whereas unstained tests were consid-

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ered as dead. Living and dead specimens were sorted by species. All species, except *Ammonia aomoriensis*, were mounted in Plummer cell slides with glue, counted and measured using an eyepiece reticle on the Wild M3C dissecting microscope. *Ammonia aomoriensis* was kept in single cell slides for further analyses.

Test morphometry of *Ammonia aomoriensis* was analyzed with an automated image analysis system using a Leica Z16 APO microscope, and analySIS software (version 5.0) at the University of Angers, France (cf. Bollmann et al., 2004; Clayton et al., 2009). Resolution of images is 2.69 µm^{-2}. Due to the oval shape of *Ammonia aomoriensis* tests, the size of tests is given as mean diameter, calculated from the minimum and maximum diameter.

The census data were standardized to population density given as individuals/tests per 10 cm^{-3} sediment. Histograms were created depicting the proportion of living *A. aomoriensis* in 11 size classes from < 50 to > 500 µm in 50 µm intervals and presented as the average of three replicates taken each month during the six months incubation time.

The dry weight of dead and living *A. aomoriensis* was measured using a microbalance with an accuracy of 1 µg (Sartorius, M3P-000V001). Dry weight per individual/test was calculated from the total dry weight divided by the total number of individuals/tests.

Finally, tests of *Armorella sphaerica* and corroded specimens of *A. aomoriensis* were photographed with a MiniPixie (MPX2051UC) digital microscope.

2.5 Electron microprobe analysis

The two ranked species, *A. aomoriensis* and *E. incertum*, were prepared for **E**lectron **M**icro**P**robe (EMP) X-ray microanalysis (JEOL JXA 8200). We focused on the visual elemental distribution of Ca and Mg on cross-sections of the tests, which were cultured at pCO_2 of 3247 µatm and retrieved after six months incubation. The advantage of this technique is high spatial resolution (±1 µm), so that single foraminiferal tests can be analyzed (Kellner et al., 1998; Glock et al., 2012).

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Tests of both species were embedded under vacuum into Araldite™ epoxy resin by using a CitoVac™ vacuum embedding system (Struehrs™). Small drops of resin were used to fill the inner part of the chambers. The tests were set under pressure to collapse air inclusions inside the resin and hardened in a drying cabinet at 60 °C.

Using the Tegra-Pol-21 system (Struehrs™), the surface of the resin was ground down by hand with alumu-silica grinding paper until the proloculus of the specimen became visible. The surface was polished with different grades of alumo-silica and diamond paste (until 1 µm grain size) on a self rotating polishing plate.

Prior to the measurement, each cross-section was carbon coated. The microprobe was operated in a wavelength dispersive mode by using different Ka X-ray lines for each element. Two different detector crystals were used for the elements Ca (crystal: PETJ) and Mg (crystal: TAPH). The acceleration voltage was 15 kV and the beam current was 20 nA. The tests of *A. aomoriensis* and *E. incertum* were mapped by 0.5 µm step size and a dwell time of 500 ms. The results are illustrated as maps of relative measured intensities for both elements.

2.6 Calculations

Carbonate production and accumulation of the major calcifying species *A. aomoriensis* have been calculated from the difference of dry carbonate weight of individuals or tests produced or accumulated during six months incubation time. The production or accumulation rate in grams refers to an area of 1 m^2 per year.

For 100 living *A. aomoriensis* from size fraction 200 to 300 µm, the total organic content, including cytoplasm and organic linings of the test, was determined by combustion off the organic material from the carbonate tests in a muffle furnace at 500 °C for 6 h. The amount of total organic content is calculated from the weight loss and given as a percentage of the total dry weight of the individuals (Table S6 in the Supplement). This value was subtracted from total weight to obtain the dry weight of shell carbonate (Table S5 in the Supplement).

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2.7 Statistics

Two-factorial ANOVA was performed with the two parameters pCO_2 and incubation time with STATISTICA 8 (Table 4). All measured raw data of each treatment were used for statistical analyses. The data are given as mean ± standard deviation.

3 Results

3.1 Carbonate chemistry

Seawater temperature and salinity were stable during the experimental period. Average temperatures ranged from 16.4 to 17.2 °C and salinities from 15.1 to 15.9 (Table 1).

Phosphate and silicate concentrations changed markedly over the course of the experiment. Phosphate concentration increased 31-fold during the first three months from 0.19 to 5.86 µmol L^{-1} (Table 1). Mean silicate concentrations were in general high with 191.98 µmol L^{-1} and exhibited a threefold increase from 138.94 to 367.19 µmol L^{-1} after two months (Table 1). By the end of the experiment, concentrations of phosphate and silicate decreased again and achieved the initial values that were observed at the beginning of the experiment. In dependency to seawater pCO_2, mean pH values ranged between 8.21 and 7.17 (Table 1) and were stable throughout the incubation period. Total inorganic carbon increased with increasing pCO_2 from 2210.5 to 2464.2 µmol L^{-1} (Table 1). The calculated mean pCO_2 levels of the treatments were thereby 430, 907, 1865 and 3247 µatm (Table 1). It has to be noted that CO_2 concentrations in the unchanged air effected a higher pCO_2, while the partial pressures at higher concentrations led to markedly lower pCO_2 levels than the target values. In the following, we refer our results to the pCO_2 levels that were prevailed in the culture vessels (Haynert et al., 2011). Mean seawater alkalinity was 2379.3 µmol kg^{-1} and did not differ significantly between the treatments (Table 1). At a pCO_2 of 1865 µatm, seawater

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Ω_{calc} values decreased partially below 1. High pCO_2 of 3247 µatm caused permanent undersaturation of Ω_{calc} with 0.57 on average (Table 1).

The carbonate chemistry measurements revealed strong differences of pCO_2 and Ω_{calc} between seawater and sediment pore water in the culture vessels (Fig. 1). The sediment pore water was characterized by higher pCO_2 and lower pH than the supernatant seawater in the culturing vessel (Fig. 1a and b). At the same time, pore water alkalinity (3127.8 µmol kg^{-1}) was much higher than the bulk seawater alkalinity (0–2 cm water depths) of 2113.1 µmol kg^{-1} and the water overlaying the sediment (2–4 cm water depths) with 2442.3 µmol kg^{-1}. The accumulation of A_T in the sediment caused a higher saturation of Ω_{calc} and even in the highest pCO_2 treatment a slight supersaturation, $\Omega_{calc} > 1$ (Fig. 1c and d, Table S1 in the Supplement).

3.2 Species composition and foraminiferal assemblages

The assemblages comprised five calcareous species: *Ammonia aomoriensis*, *Elphidium excavatum excavatum*, *Elphidium excavatum clavatum*, *Elphidium gerthi* and *Elphidium incertum*, and the arenaceous species *Ammotium cassis*, *Reophax dentaliniformis* and *Armorella sphaerica* (Tables 2 and 3, Fig. 2).

The fauna was dominated by *A. aomoriensis* with 99 % of the living fauna and 85 % in the dead fauna, whereas *E. incertum* was rare with 1 % of living individuals and 7 % of dead tests (Tables 2 and 3). All other species were very rare or were only occasionally found in the foraminiferal assemblages. Accordingly, we will focus on the dominant calcareous species *A. aomoriensis* in the following.

3.2.1 Population density, test diameter and reproduction of living *Ammonia aomoriensis*

The population density and size-frequency distribution exhibited strong variations due to growth, reproduction and mortality of foraminiferal faunas during the six months incubation. Incubation time had a significant effect on test diameter of living *A. ao-*

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moriensis ($F(5,45) = 18.14$, $p < 0.01$) whereas pCO_2 had no effect as a single factor ($F(3,45) = 0.61$, $p > 0{,}05$,Table 4). However, the interaction of both, pCO_2 and incubation time was significant ($F(15,45) = 2.14$, $p < 0.03$). The size distribution revealed growth cohorts which were characterized by a fixed, simultaneously reproduction period. A further character of a cohort was the similar increase of test diameter and the loss of individuals by death during the same period.

Initial population density of living *A. aomoriensis* fauna varied from 342 to 583 ind. $10\,cm^{-3}$ (Table S2 in the Supplement) and the mean test diameter per treatment ranged from 169 to 182 µm (Table S2 and 8 in the Supplement). Lowest mean population densities were observed in the 430 µatm treatment with 295 ind. $10\,cm^{-3}$, intermediate with 367 and 407 ind. $10\,cm^{-3}$ in 907 and 3247 µatm pCO_2-treatments, and highest mean densities of 524 ind. $10\,cm^{-3}$ at a pCO_2 of 1865 µatm (Table S2 in the Supplement). Whereas the population density at 430 µatm was relatively stable, the density fluctuated considerably in the 907, 1865 and 3247 µatm pCO_2-treatments (Fig. 3). *Ammonia aomoriensis* density declined strongly during the first month at pCO_2 of 1865 and 3247 µatm. An explosive increase of living *Ammonia aomoriensis* up to 610, 1378 and 518 ind. $10\,cm^{-3}$ was observed at pCO_2 of 907, 1865 and 3247 µatm after three months. A further increase up to 602 ind. $10\,cm^{-3}$ followed at 3247 µatm after five months (Fig. 3a, Table S2 in the Supplement). The strong increase of population densities correlated with dominant reproduction events at 1865 µatm after three months, and two sequent reproduction events at pCO_2 of 3247 µatm after three and four months as indicated by the occurrence of high numbers of small individuals with a test diameter < 100 µm (Fig. 4, Table S3 in the Supplement). A less pronounced reproduction event in the background was observed at a pCO_2 of 907 µatm after four and five months, though population densities were not affected (Fig. 4, Table S3 in the Supplement). *Ammonia aomoriensis* was able to reproduce from size class of 250 µm up to 350 µm, at 350 µm 40 % of the cohorts had reproduced. After reproduction, the growth of individuals at 1865 µatm led to an increase of the mean test diameter from 185 to 287 µm until the end of the experiment (Table S4 in the Supplement). The mean growth of *A.*

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aomoriensis varied between 25 and 38 µm per month during incubation, at the beginning specimens grew by up to 50 µm within one month.

3.2.2 Abundance and test diameter of dead *Ammonia aomoriensis*

The abundance of the dead fauna ranged from 24 to 61 tests 10 cm^{-3}. At pCO_2-levels of 430 and 907 µatm, their abundance increased steadily until the 4th and 5th month, and subsequently decreased until the end of experiment (Fig. 3b, Table S2 in the Supplement). In contrast, at pCO_2 of 1865 and 3247 µatm, the number of *A. aomoriensis* tests did not significantly change until the 4th month (Fig. 3b). Afterwards, the number of empty tests increased by 80 % at 1865 µatm until the end of the experiment (Table S2 in the Supplement). These results correlated with a strong decline of population densities from 1378 to 338 ind. 10 cm^{-3} from the third to the fifth month (Fig. 3a). At 3247 µatm, test abundance decreased to 32 tests 10 cm^{-3} at the end of the experiment (Table S2 in the Supplement).

The mean test diameter ranged between 290 and 283 µm at pCO_2 from 430 to 1865 µatm. At higher pCO_2 of 3247 µatm, test diameter was clearly lower with 258 µm (Table S4 in the Supplement) which indicated a frequent mortality of large and adult foraminifera up to 1865 µatm, whereas at higher pCO_2 a frequent mortality of smaller and younger individuals was recognized. Test diameter of dead *A. aomoriensis* was significantly effected by incubation time ($F(5,46) = 16.65$, $p < 0.01$) but not by pCO_2 ($F(3,46$, $p > 0,05$) (Table 4).

3.3 Dry test weight

The initial dry weight per individual of living *A. aomoriensis* was 1.56 µg on average (Fig. 6, Table S5 in the Supplement). With increasing test diameter, the dry weight per living individual increased constantly, but no significant differences of dry weight-diameter ratio were observed between the different pCO_2 treatments (Fig. 5a). Dry weight per individual increased by 68, 57, 70 and 62 % at a pCO_2 of 430, 907, 1865

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and 3247 µatm respectively until the first month (Table S5 in the Supplement). At 430 and 3247 µatm, dry weight per individual did not change significantly any more until the end of the experiment (Table S5 in the Supplement). In contrast, the dry weight of *A. aomoriensis* increased up to 7.30 µg at a pCO_2 of 907 µatm after two months (Table S5 in the Supplement), which correlated with an increase in test diameter by 116 µm on average (Fig. 4). At a pCO_2 of 1865 µatm, dry weight per individual decreased significantly to 1.30 µg after three months (Table S5 in the Supplement). These results correlated with the reproduction events and resulting dominance of small foraminifera of size classes < 50 up to 200 µm (Fig. 4).

In comparison to living *A. aomoriensis*, mean dry weight per empty test was higher with 6.18 µg on average (Fig. 6, Table S5 in the Supplement). This probably results from the more frequent reproduction or mortality of large specimens. Similar to the dry weight of specimens from the living fauna, no effect of any pCO_2 was observed with empty tests (Fig. 5b). In accordance to changes in test diameter, the average dry weight per test changed during the experiment. At 430 and 907 µatm, dry weight per test increased by 60 and 50 % until the second month and remained stable with mean values of 5.63 and 5.84 µg until the end of the experiment (Table S5 in the Supplement). In pCO_2-treatments 1865 and 3247 µatm, dry test weight increased by 41 and 71 % during the first month (Fig. 6b), followed by a further slight increase up to 7.73 µg at 1865 µatm after five months (Table S5 in the Supplement). These observations were in agreement to the decline of population densities of *A. aomoriensis* after the first and fifth month at 1865 µatm (Fig. 3a).

3.4 Carbonate production and accumulation

The total organic content of living individuals was found to be 4.3 %, which was subtracted from total dry weight in order to determine the absolute amount of $CaCO_3$ (cf. Movellan et al., 2012) (Table S5 in the Supplement). Production is considered as weight increase measured at subsequent sampling. Average production during the entire incubation period is given as mean value of monthly weight increases. Living

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A. aomoriensis exhibited the lowest mean $CaCO_3$ production of 595 µg at the lowest pCO_2 of 430 µatm, following by 886 µg at the highest pCO_2 of 3247 µatm after six months incubation. The three replicate treatments of 907 and 1865 µatm showed similarly higher mean $CaCO_3$ production of 1269 and 1256 µg with a total culture vessel area of 42.25 cm^2 and an incubation time of six month. The calculated total carbonate production rate for living individuals was 0.47 $g\,m^{-2}\,yr^{-1}$ (Table S6 in the Supplement).

The $CaCO_3$ accumulation of empty tests varied between the pCO_2 treatments (Table S6 in the Supplement). The highest rate of 908 µg $CaCO_3$ was observed at 907 µatm, followed by 670 µg at 430 µatm. With increasing pCO_2 of 1865 and 3247 µatm, $CaCO_3$ rates decline to 435 and 239 µg after six months incubation with the above specified settings. The calculated total carbonate accumulation of empty tests was 0.27 $g\,m^{-2}\,yr^{-1}$ (Table S6 in the Supplement).

3.5 Observations of test structures and elemental distribution

At high pCO_2 of 3247 µatm, light micrograph images of dead *A. aomoriensis* showed that most of the tests were completely destroyed during the last two months of the experiment. The strongest effect of test degradation was the charistic star-like appearance, which left only the umbilicus area and the suture of the chambers intact.

Cross-sections of test walls of *A. aomoriensis* (Fig. 7a) and *E. incertum* (Fig. 7b) revealed that the tests of both species were composed of a single calcium carbonate layer, which contained high Ca and low Mg calcite. In comparison to *E. incertum*, *A. aomoriensis* exhibited a higher Mg-content. Furthermore, the test wall of *A. aomoriensis* was highly porous, whereas *E. incertum* showed a smooth surface without any visible porosity.

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4 Discussion

This study describes the impact of elevated pCO_2 on a natural foraminiferal community from the southwestern Baltic Sea which was exposed to 4 different pCO_2 levels for six months. It is the first study to investigate the multi-generational response using natural sediment with living foraminiferal fauna of natural composition. The foraminiferal community developed and reproduced normally in all treatments, as the specific sediment chemistry caused, compared to the bulk seawater, a relative high saturation state with respect to omega calcite, and thereby prevented the tests of living individuals from dissolution.

4.1 Sediment chemistry

The sediment used in this experiment was sampled from Kiel Fjord, western Baltic Sea, which is rich in organic matter (Nikulina et al., 2008). During the experiment, a layer of organic detritus formed at the sediment–water interface. Organic substances influence the microbial activity, the rates and pathways of organic matter remineralization and nutrient recycling (Jonsson et al., 1990; Conley and Johnstone, 1995), and thereby influenced the underlying sediment chemistry (Graf et al., 1984). The remineralization of organic matter is mainly attributed to a wide array of hydrolytic and fermentative bacteria (Turley et al., 2000), which break complex multi-carbon compounds down to smaller, more soluble and digestible substances. Bacterial activity is often attributed as a limiting step in degradation of organic matter and extent of degradation (Tyson, 1995; Arnosti, 2004).

It is conceivable that silicate and phosphate concentrations were highly variable in the stagnated water body of the culture vessels throughout the experiment due to the high microbiological activity. Concentrations of both nutrients increased during the first two months and afterwards decreased until the end of the experiment.

One aspect could be the disturbance of the sediment after homogenization at the beginning of the experiment. This process could cause a remobilization of the bounded

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nutrients in the pore water, which diffused gradually through the filter of the nepheloid layer. This in turn would increase nutrient concentration increased in the overlying seawater.

However, silicate concentrations remain relatively high. Microscopic analysis showed that the detritus-layer was composed of centric diatoms, which also dominated in the natural environment. The algal material of *Nannochloropsis oculata*, *Phaeodactylum tricornutum* and *Chlorella* added as food did not accumulate on the sediment surface. This in turn could imply that the added algae material was directly dissolved, which could explain the high silicate concentrations. Otherwise, increasing silicate concentrations may result from remineralization of diatoms (Conley and Johnstone, 1995). Sediment samples were taken in April, when high nutrient and productivity is usually encountered (Wulff et al., 1986, 1990; Elmgren, 1989; Wollast, 1998; Thomas et al., 2003; Pätsch and Kühn, 2008). The spring bloom, ranging from the end of February to early April in the southwestern Baltic Sea, is dominated by diatoms, therefore maximal diatom biomass and biogenic silica flux to the sea floor (Wasmund et al., 2005, 2006). After deposition at the sediment surface, remineralization of the dead diatoms may have caused a substantial increase of silicate in the culture vessels during the experiment (Conley and Johnstone, 1995).

The high degradation of organic matter such as diatoms may have also caused an increase of phosphate concentrations (Balzer, 1986). In oxic sediments dissolved inorganic phosphate (DIP), is usually bound to calcium, chemisorbed by ironoxyhydroxides in distinct iron compounds and causes high phosphate accumulations in the sediment (Nissenbaum, 1979; Filipek and Owen, 1980; Krom and Berner, 1981). However, high O_2 consumption by degradation of organic matter may have reduced the oxygen concentrations in the sediment, resulting in mobilization of DIP from sediments (Krom and Berner, 1981). The decrease of both nutrients until the end of the experiment may have arisen from bacterial microbiological activity of bacteria, although this aspect has not yet been sufficiently studied.

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Degradation processes of organic matter at the sediment–water interface consumed O_2 and produced CO_2, and thus resulted in higher sediment pore water pCO_2in comparison to the seawater. Similarly, the sediment was characterized by much higher alkalinity values than the seawater (3127 vs. 2379 µmol kg^{-1}). Both aerobic or anaerobic degradation of organic matter release dissolved inorganic carbon (DIC). Whereas aerobic degradation has no significant effect, anaerobic degradation increases alkalinity (A_T) by denitrification and sulfate reduction (Yao and Millero, 1995; Thomas et al., 2009). Therefore, we assume that O_2 consumption at the sediment–water interface exceeded the delivery of O_2 via diffusion, which could induce anaerobic conditions in the sediment pore water. A dark grey sediment layer on the bottom of the culture vessels supported our assumption. This in turn enhances the CO_2 buffer capacity and consequently causes a relatively high Ω_{calc} (Thomas et al., 2009). These differences of the carbonate chemistry between water column and sediment was in agreement with observations from field studies (Thomas et al., 2009; Haynert et al., 2012).

4.2 Foraminiferal communities

The species composition of living and dead assemblages which were used in the experiment were similar to the assemblages prevailing in Kiel and Flensburg Fjords (Nikulina et al., 2008; Polovodova et al., 2008, 2009; Haynert et al., 2012).

At the beginning of the experiment, the population density of the living fauna (433 ind. 10 cm^{-3}) was very similar to the mean population density of 448 ind. 10 cm^{-3}, found in the nearby sampling station PF15-13 in December 2005 (Nikulina et al., 2008; Polovodova et al., 2008). The living assemblages at both stations were dominated by *A. aomoriensis* (*A. beccarii* of Nikulina et al., 2008). In December 2005, *E. excavatum clavatum* was common and *E. excavatum excavatum* and *E. incertum* were rare, whereas in April 2011, the living fauna consisted almost exclusively of *A. aomoriensis*. These differences were probably caused by the interannual variation in the community structure (Lutze, 1974; Wefer, 1976; Polovodova et al., 2009; Haynert at al., 2012).

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The dominance of living *A. aomoriensis* is probably explained by the diatom dominated spring bloom, which enables high food supply and thereby facilitates reproduction. A similar relationship between diatom spring blooms and reproduction events was reported for *E. excavatum clavatum* at deeper waters off Boknis Eck, southwestern Baltic Sea (Schönfeld and Numberger, 2007).

In addition, the arenaceous species *Armorella sphaerica* occurred by incident in the set up. The species was recorded in Kiel Bay by Rhumbler (1935) and later by Brodniewicz (1965) in the southern Baltic Sea. Its sporadic occurrence and sudden appearance in our experiment could be explained by the activation of dormant propagules (Alve and Goldstein, 2002). Alternatively, the species may be widespread but rare in Kiel Fjord, and so have been overlooked in previous studies. In our experiment, however, suitable conditions, such as food supply and oxygenation could have induced the activation of resting stages.

4.3 Response of *Ammonia aomoriensis* life cycle

In the first month of the experiment, population densities of living *A. aomoriensis* declined strongly at a pCO_2 of 1865 and 3247 µatm. This decline might indicate conditions of $\Omega_{calc} < 1$ in the sediment. The sediment was put in the vessels 20 days prior to CO_2 manipulation. Nevertheless, the remineralization processes in the sediment were still ongoing as indicated by the strong increases of seawater phosphate and silicate concentration during the first two months. Therefore, high pore water alkalinity and thereby supersaturation of calcium carbonate might have not been established in the early phase of the experiment. Undersaturation has been already shown to decrease growth of *A. aomoriensis* and thereby increase mortality and test dissolution (Haynert et al., 2011). Similarly, a decrease of *Ammonia* species growth was observed with decreasing $[CO_3^{2-}]$, respectively $\Omega_{calc} < 1$ (Keul et al., 2013).

During the course of the experiment, however, the progressing remineralization processes in the sediment may have increased saturation state above 1. Accordingly, *A.*

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aomoriensis was relatively unaffected by high pCO_2 later on and continued to grow and reproduce, even under highly elevated pCO_2 conditions (Haynert et al., 2012).

In comparison, previous ocean acidification studies cultured living benthic foraminifera without their natural sediment (Le Cadre et al., 2003; Kuroyanagi et al., 2009; Dissard et al., 2010; Allison et al., 2010; Haynert et al., 2011; Fujita et al., 2011; Vogel and Uthicke, 2012; Keul et al., 2013; McIntyre-Wressnig et al., 2013). Under these laboratory conditions, foraminifera were directly exposed to the seawater which might result in low and even undersaturation of omega calcite at high seawater pCO_2 (Haynert et al., 2011).

The current study underscores, that endobenthic foraminifera from marginal low saline habitats responded completely different under elevated pCO_2 in culturing experiments, depending whether they were kept with or without their natural sediment. Furthermore, high or low organic matter content of the substrate, grain size composition (Conley and Schelske, 1989), bacterial remineralization (Turley et al., 2000), and oxic or anoxic conditions (Jonsson et al., 1990) play a certain role in sediment and pore water chemistry, and thereby may influence the living conditions of benthic communities. In fine-grained sediments with a high content of organic substances these processes play an important role for the foraminiferal microhabitat. It is reasonable to assume that the effects on carbonate chemistry are less pronounced in coarse sediments. These results emphasize the importance to understand the sediment carbonate chemistry in the context of their natural settings.

During the six months incubation, the populations of all treatments revealed strong variations of their density and size-frequency distribution due to growth, mortality and reproduction events. The shift of mean size distribution between the monthly sampling intervals enabled the calculation of growth rates which varied between 25 and 38 µm per month and agreed with earlier growth rates estimates reporting 13 to 39 µm (Haynert et al., 2011). This growth corresponds to the addition of one or two chambers per month, as one added chamber equates 27 ± 16 µm in test diameter (Haynert et al., 2011). An earlier study described, growth rate as being uniform in all size classes.

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Small individuals grow more rapidly, whereas adult individuals slow down the growth before reproduction (Bradshaw, 1957). Furthermore, changing habitat conditions, in particular food supply, play an important role at chamber formation (Bradshaw, 1961). It appears plausible that larger and a greater number of chambers will be formed under favorable conditions.

Size distributions of tests revealed that most of the individuals reproduced or died at a mean size of 285 µm at a pCO_2 ranging from 430 to 1865 µatm. At the highest pCO_2 of 3247 µatm, mean test diameter was slightly lower with 258 µm. Apart from growth, reproduction events had a pronounced effect on the mean size of the population. Cohorts of small, juvenile individuals (< 100 µm) could be identified. Whereas reproduction events could not be detected at 430 µatm, strong cohorts with high numbers of individuals were observed at 1865 and 3247 µatm, with a strongest variability at 1865 µatm.

Ammonia aomoriensis reproduced at sizes between 250 µm and 350 µm. At 350 µm, 40 % of the cohorts either have reproduced or died. These results agreed with a previous study of Bradshaw (1957) where the mean test diameter of *Streblus beccarii* var. *tepida* ranged between 266 and 357 µm at reproduction. In dependency of environmental conditions, reproduction follows approximately 28-day intervals with about 28 young juveniles per parent under optimal conditions (Bradshaw, 1957). In the current study we observed reproduction events, but the different cohorts made it impossible to determine exactly either the intervals of reproduction or the number of juveniles per parent.

In dependency of asexual and sexual reproduction, the generations consisted of different forms as influenced by test dimorphism (Murray, 2012). The megalospheric form is the result of asexual reproduction, whereas the microspheric form is the product of sexual reproduction (Lister, 1903). However, the reproduction of *A. aomoriensis* is insufficiently studied to date and further field and laboratory experiments would be necessary to better understand the life cycle of *A. aomoriensis*, and the species specific variability of *Ammonia* in general. However, since reproduction was observed in all pCO_2 treatments, the conditions prevailing in the sediment were sufficient to allow

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successful reproduction even at 3247 µatm pCO_2. This supports findings that natural foraminiferal communities in the southwestern Baltic Sea can withstand permanent high pCO_2 levels of above 2000 µatm when they are fully sheltered in fine-grained sediment (Haynert et al., 2012).

4.4 Carbonate production of *Ammonia aomoriensis*

The carbonate production of benthic foraminifera was described in previous studies (e.g. Phleger and Soutar, 1973; Muller, 1974; Wefer and Lutze, 1978; Hallock, 1981; Bosence, 1989; Langer et al., 1997) which determined the foraminiferal carbonate content of sediment samples from different habitats. In contrast, in our study the main focus was on living benthic foraminifera containing cytoplasm. Little is known about the fractions of cytoplasm and tests weight in benthic foraminifera. The estimated total organic content in living *A. aomoriensis* is 4.3 % of total dry weight which is in agreement with the estimated protein content of 20 % and 5 % organic dry content in *Ammonia tepida* (Movellan et al., 2012). The study of Wefer and Lutze (1976) observed a ratio of 1 : 1 of protoplasm and test weight in benthic foraminifera which referred to wet weight (see Table 1 in Wefer and Lutze, 1976) The cytoplasm water content plays an important role in this determination as TEM micrograph images documented a high amount of seawater vacuoles in the foraminifera chambers (see Fig. A3.3.2 in Glock, 2011). Therefore, and in agreement with A. Movellan (personal communication, 2013), we assume a water content of approximately 76 % in foraminiferal cytoplasm. However, the percentage of water and cytoplasm content varies in relation to test size and weight, and due to the natural variability of the microenvironment and the species-specific morphometry (Movellan et al., 2012).

The carbonate production of living *A. aomoriensis* amounts 0.47 $g\,m^{-2}\,yr^{-1}$, whereas the carbonate accumulation of dead tests equates 0.27 $g\,m^{-2}\,yr^{-1}$ during the incubation time. This estimate of $CaCO_3$ production is much higher than those reported for natural foraminiferal assemblages in the western Baltic Sea. Production rates of calcareous benthic foraminifera rates ranged from 0.01 to 0.03 $g\,m^{-2}\,yr^{-1}$ in the shallow

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water habitat from 5–15 m depth of Kiel Bay (Wefer and Lutze, 1978). However, this low carbonate production was probably caused by a strong seasonality of food supply and mechanical stress on shoals with lag sediments, where these samples were taken. Muddy sediments such as in Kiel Fjord, with high organic matter content as potential source of food, showed a markedly higher foraminiferal carbonate production of up to 3.12 g m^{-2} yr^{-1} (Wefer and Lutze, 1978; Nikulina et al., 2008). Therefore, both favorable food supply and sustaining high population densities during the incubation facilitated the observed high $CaCO_3$productivity of *A. aomoriensis*.

Not less than 36 % of the produced tests are accumulated in the sediment, which is obviously higher as reported by Wefer and Lutze (1978), the accumulation rate ranged between 0 and 4 % in the natural habitat. In the transitional environments from fine sand to mud, the accumulation rate varied from 1 to 1.2 % (see Table 2 in Wefer and Lutze, 1978). Under natural conditions, mechanical forces play an important role and affected the tests, as well as dissolution and ingestions by macro- and meiofauna (Wefer and Lutze, 1978). In the present study, *A. aomoriensis* was cultivated in a protective habitat without any mechanical impacts of the empty tests, therefore a higher accumulation rate was recorded.

4.5 Impact on foraminifera tests

Living *A. aomoriensis* and *E. incertum* exhibited no dissolution features during the whole incubation time. The conditions in the natural sediment create a protective microhabitat for benthic foraminifera with a relatively high calcium carbonate saturation state. These observations are in contrast to previous laboratory studies, where *A. aomoriensis* and *A. beccarii* exhibited a relationship between pCO_2, respectively pH, and test degradation (Le Cadre, 2003; Haynert et al., 2011). In comparison to the present study, living foraminifera were isolated from their natural sediment, therefore the tests of living specimens were directly affected by the carbonate chemistry conditions of the seawater.

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However, some empty tests of *A. aomoriensis* were destroyed at a pCO_2 of 3247 µatm during the last two months of incubation. This may be because high pCO_2 and unfavorable $\Omega_{calc} < 1$ reduced the average diameter. In contrast, empty tests of *E. incertum* showed no signs of dissolution. This species specific response agrees well with our field observation from Flensburg Fjord (Haynert et al., 2012). In order to explain these differences, cross sections of both species were analyzed using EMP. The element maps suggested that tests of both foraminiferal species are composed of a single layer of secondary calcite, which is characterized by a relative low Mg-content (Erez, 2003). In comparison to *E. incertum*, the test of *A. aomoriensis* displayed a higher Mg-content and was highly porous. The crystals, rich in Mg are oriented in a structure of small radial needles (Hansen and Reiss, 1972; Bellemo, 1974), which are sensitive and dissolved first at undersaturated conditions. In combination with a greater test surface, *A. aomoriensis* was therefore less resistant to dissolution than *E. incertum*. EMP observations are thus considered to provide valuable constraints for the sensitivity of a species towards dissolution stress.

5 Conclusions

In the present ocean acidification study, benthic foraminifera were cultured in their natural sediment over a period of several generations. Under those laboratory conditions, the alkalinity (A_T) and therefore the CO_2 buffer capacity in the sediment differed strongly from the conditions in the water column. Thereby the sediment chemistry created a microhabitat that supported the growth and development of a benthic foraminiferal community even at highly elevated pCO_2. Fine-grained sediments with high organic matter content facilitated a high carbonate production of *A. aomoriensis*. Growth, reproduction and mortality of *A. aomoriensis* were unaffected by elevated pCO_2. Consequently, under the current microhabitat conditions, the dominant *Ammonia aomoriensis* could maintain an important role in benthic carbonate production and accumulation in the southwestern Baltic Sea. However, at high pCO_2 and slight undersaturation of Ω_{calc},

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empty tests of *A. aomoriensis* were subjected to dissolution, whereas empty *E. incertum* tests remained intact. The species specific response might be explained by differences in test composition and microstructure. These results emphasize the importance to understand the sediment carbonate chemistry in the natural environment of benthic foraminifera, which depend on sediment type, grain size, organic matter, remineralization and chemical conditions in the pore water. In Kiel Fjord, organic-rich and fine-grained sediments prevail which influence the pore water carbonate chemistry, and thereby provide a stable habitat for benthic foraminifera. Due to these characteristics, foraminiferal communities withstand present day, seasonally high pCO_2 levels and might be also be able to tolerate moderate future pCO_2 increases.

Supplementary material related to this article is available online at: http://www.biogeosciences-discuss.net/10/9523/2013/bgd-10-9523-2013-supplement.pdf.

Acknowledgements. This study was funded by the German Research Foundation (grant SCHO605/7–1). The authors are grateful to the crew of RB Polarfuchs for help with sampling in Kiel Fjord. We acknowledge Torben Struve for help with sampling and planning the design of experimental set up, Cara Nissen for supporting the water chemistry measurements, Gitta Ann von Roenn, Eva Klünker and Julia Langer for support during endless hours of picking. We thank Anna Jentzen (GEOMAR) for help with the automatic analysis measurements at the University of Angers. We thank Mario Thöner (GEOMAR) for technical support on the Electron Micro Probe analyzer. Frank Melzner (GEOMAR) and Ulf Riebesell (GEOMAR) provided the climate room and laboratory facilities during experimental time.

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

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Table 1. Carbonate chemistry parameters of each pCO_2-treatment in the culture vessels. Total alkalinity (A_T), partial pressure of CO_2(pCO_2) and saturation state of calcite (Ω_{calc}) were calculated from measured temperature, salinity, pH_{NBS}, total carbon (C_T), phosphate (PO_4^{3-}) and silicate (Si). The standard deviation (1-sigma) refers to replicate measurements.

pCO_2-values of gas (µatm)	Incubation time (months)	Seawater measurement T (°C)	S	pH_{NBS}	C_T (µmol kg^{-1})	PO_4^{3-} (µmol L^{-1})	Si (µmol L^{-1})	Calculations from pH_{NBS} and C_T A_T (µmol kg^{-1})	pCO_2 (µatm)	Ω_{calc}
380	0	16.8 ± 0.05	15.7 ± 0.05	8.19 ± 0.01	2202.3	0.17 ± 0.02	139.24 ± 3.83	2377.5	359	3.98
	1	16.6 ± 0.05	15.8 ± 0.04	8.09 ± 0.01	2277.0	3.52 ± 0.26	262.17 ± 1.11	2422.5	472	3.30
	2	16.4 ± 0.05	15.9 ± 0.30	8.01 ± 0.01	2276.5	5.87 ± 0.10	366.76 ± 1.92	2397.0	568	2.75
	3	16.8 ± 0.16	15.5 ± 0.04	8.21 ± 0.00	2252.2	1.97 ± 0.04	144.35 ± 2.04	2439.8	352	4.23
	4	17.2 ± 0.24	15.3 ± 0.08	8.13 ± 0.01	2250.6	1.60 ± 0.01	149.94 ± 1.77	2406.0	425	3.62
	5	16.5 ± 0.00	15.1 ± 0.04	8.10 ± 0.01	2108.4	0.93 ± 0.26	138.26 ± 0.52	2238.4	430	3.06
	6	16.7 ± 0.06	15.2 ± 0.06	8.12 ± 0.00	2106.7	0.16	138.09	2245.6	406	3.25
1120	0	16.8 ± 0.04	15.6 ± 0.04	7.87 ± 0.02	2420.0	0.18 ± 0.01	138.36 ± 2.94	2487.6	851	2.15
	1	16.6 ± 0.05	15.8 ± 0.04	7.80 ± 0.01	2489.7	3.31 ± 0.09	261.87 ± 1.22	2545.5	1005	1.92
	2	16.4 ± 0.05	15.8 ± 0.04	7.78 ± 0.01	2389.0	5.82 ± 0.06	367.33 ± 0.67	2439.6	1022	1.73
	3	16.9 ± 0.10	15.5 ± 0.04	7.87 ± 0.01	2441.8	1.91 ± 0.08	148.48 ± 8.29	2514.6	842	2.22
	4	16.7 ± 0.14	15.6 ± 0.10	7.83 ± 0.02	2335.5	1.68 ± 0.17	150.47 ± 0.44	2391.7	897	1.89
	5	16.4 ± 0.05	15.2 ± 0.05	7.83 ± 0.01	2236.3	1.18 ± 0.42	139.61 ± 0.14	2286.9	867	1.77
	6	16.6 ± 0.06	15.2 ± 0.22	7.82 ± 0.00	2205.9	0.16	138.92	2254.8	866	1.74
2400	0	16.8 ± 0.04	15.6 ± 0.04	7.54 ± 0.02	2411.5	0.19 ± 0.03	140.00 ± 3.76	2389.7	1786	1.02
	1	16.6 ± 0.04	15.8 ± 0.00	7.47 ± 0.00	2539.7	3.32 ± 0.28	261.57 ± 1.75	2499.0	2210	0.90
	2	16.5 ± 0.05	15.8 ± 0.04	7.43 ± 0.01	2452.7	5.85 ± 0.12	368.11 ± 0.50	2404.9	2330	0.79
	3	16.8 ± 0.09	15.5 ± 0.04	7.54 ± 0.00	2407.0	2.00 ± 0.12	149.52 ± 8.27	2385.3	1810	1.00
	4	16.5 ± 0.15	15.3 ± 0.10	7.52 ± 0.01	2394.5	1.59 ± 0.02	150.12 ± 0.79	2365.7	1882	0.94
	5	16.5 ± 0.00	15.2 ± 0.05	7.62 ± 0.00	2291.0	0.87 ± 0.05	140.33 ± 0.38	2289.0	1427	1.13
	6	16.7 ± 0.06	15.2 ± 0.06	7.57 ± 0.00	2298.5	0.15	139.21	2283.5	1607	1.02
4000	0	16.8 ± 0.05	15.6 ± 0.04	7.32 ± 0.04	2496.5	0.21 ± 0.02	138.14 ± 2.83	2407.2	3031	0.63
	1	16.6 ± 0.05	15.8 ± 0.00	7.31 ± 0.01	2564.9	3.79 ± 0.32	262.93 ± 2.24	2472.8	3179	0.63
	2	16.4 ± 0.05	15.8 ± 0.03	7.17 ± 0.01	2492.9	5.90 ± 0.17	366.55 ± 0.88	2353.5	4178	0.43
	3	16.6 ± 0.05	15.5 ± 0.05	7.34 ± 0.00	2573.5	2.12 ± 0.33	154.18 ± 9.51	2489.1	2983	0.67
	4	17.1 ± 0.34	15.4 ± 0.03	7.30 ± 0.02	2461.2	1.59 ± 0.03	150.34 ± 0.74	2366.2	3178	0.59
	5	16.5 ± 0.05	15.1 ± 0.05	7.32 ± 0.01	2327.4	1.07 ± 0.04	133.99 ± 0.70	2240.8	2870	0.56
	6	16.6 ± 0.06	15.2 ± 0.06	7.25 ± 0.01	2332.8	0.17	136.62	2225.0	3310	0.49

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Table 2. List of living foraminifera collected from each culture vessel during six month incubation time, size fraction 63-2000 µ m.

pCO_2-treatment	Living foraminiferal species > 63 µm	Months Jun	%	Jul	%	Aug	%	Sep	%	Oct	%	Nov	%	Dec	%
430_A	Species														
	Ammonia aomoriensi	68	100.0	64	94.	50	94.	28	100.0	42	100.0	17	100.0	39	100.0
	Elphidium excavatum excavatu				0.3										
	Elphidium excavatum clavatum				0.1										
	Elphidium incertum			33	4.9	28	5.3								
	Total number of calcareous individuals	68		67		52		28		42		17		39	
	Reophax dentaliniformi														
	Total number of agglutinated individuals														
	Total number of living specimens	68		67		52		28		42		17		39	
	Species number														
	Sediment volume (cm^3)	15.		15.		15.		15.		15.		15.		15.	
	Population density (ind. 10 cm^{-3})	449.0		444.4		347.8		188.7		278.1		11.		261.7	
430_B	Species														
	Ammonia aomoriensi	40	100.0	48	93.	44	97.	60	100.0	39	96.	46	100.0	33	98.
	Elphidium excavatum excavatu				0.4										
	Elphidium excavatum clavatum														
	Elphidium incertum			32	6.2	13	2.8			14	3.4				2.0
	Total number of calcareous individuals	40		51		46		60		40		46		34	
	Reophax dentaliniformi														
	Total number of agglutinated individuals														
	Total number of living specimens	40		51		46		60		40		46		34	
	Species number														
	Sediment volume (cm^3	15.		15.		15.		15.		15.		15.		15.	
	Population density (ind. 10 cm^{-3})	265.6		339.3		303.7		396.4		268.2		302.4		225.5	
430_C	Species														
	Ammonia aomoriensi	47	100.0	70	95.	68	100.0			23	100.0	42	98.		
	Elphidium excavatum excavatu				0.1										
	Elphidium excavatum clavatum														
	Elphidium incertum			30	4.1								1.2		
	Total number of calcareous individuals	47		73		68				23		42			
	Reophax dentaliniformi														
	Total number of agglutinated individuals														
	Total number of living specimens	47		73		68				23		42			
	Species number														
	Sediment volume (cm^3)	15.		15.		15.				15.		15.			
	Population density (ind. 10 cm^{-3})	310.3		484.5		449.0				155.8		279.4			

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Table 2. Continued.

pCO_2-treatment	Living foraminiferal species > 63 µm	Months Jun	%	Jul	%	Aug	%	Sep	%	Oct	%	Nov	%	Dec	%
907_A	Species														
	Ammonia aomoriensi	54	100.0	93	98.	20	100.0	78	100.0	63	100.0	36	100.0	38	100.0
	Elphidium excavatum excavatu														
	Elphidium excavatum clavatum														
	Elphidium incertum			13	1.4										
	Total number of calcareous individuals	54		95		20		78		63		36		38	
	Reophax dentaliniformi														
	Total number of agglutinated individuals														
	Total number of living specimens	54		95		20		78		63		36		38	
	Species number														
	Sediment volume (cm^3)	15.		15.		15.		15.		15.		15.		15.	
	Population density (ind. $10\,cm^{-3}$)	357.0		625.2		134.1		518.1		414.2		238.0		255.1	
907_B	Species														
	Ammonia aomoriensi	85	100.0	62	98.	20	100.0	94	100.0			32	100.0	32	100.0
	Elphidium excavatum excavatu														
	Elphidium excavatum clavatum														
	Elphidium incertum				1.3										
	Total number of calcareous individuals	85		62		20		94				32		32	
	Armorella sphaeric														
	Reophax dentaliniformi														
	Total number of agglutinated individuals														
	Total number of living specimens	85		62		20		94				32		32	
	Species number														
	Sediment volume (cm^3)	15.		15.		15.		15.				15.		15.	
	Population density (ind. $10\,cm^{-3}$)	562.1		412.9		136.8		622.0				211.0		210.4	
907_C	Species														
	Ammonia aomoriensi	41	100.0	40	98.	1014	100.0	1051	100.0	39	100.0	46	100.0		
	Elphidium excavatum excavatu				0.2										
	Elphidium excavatum clavatum														
	Elphidium incertum				1.2										
	Total number of calcareous individuals	41		41		1014		1051		39		46			
	Reophax dentaliniformi														
	Total number of agglutinated individuals														
	Total number of living specimens	41		41		1014		1051		39		46			
	Species number														
	Sediment volume (cm^3)	15.		15.		15.		15.		15.		15.			
	Population density (ind. $10\,cm^{-3}$)	269.6		271.5		666.7		691.0		256.4		303.7			

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Table 2. Continued.

pCO_2-treatment	Living foraminiferal species > 63 µm	Months Jun	%	Jul	%	Aug	%	Sep	%	Oct	%	Nov	%	Dec	%
1865_A	Species														
	Ammonia aomoriensi	72	100.0	10	100.0	16	100.0			67	100.0	1209	100.0	84	100.0
	Elphidium excavatum excavatu														
	Elphidium excavatum clavatum														
	Elphidium incertum														
	Total number of calcareous individuals	72		10		16				67		1209		84	
	Ammotium cassi														
	Reophax dentaliniformi														
	Total number of agglutinated individuals														
	Total number of living specimens	72		10		16				67		1209		84	
	Species number														
	Sediment volume (cm^3)	15.		15.		15.				15.		15.		15.	
	Population density (ind. $10\,cm^{-3}$)	478.6		66.		106.5				443.1		794.9		555.6	
1865_B	Species														
	Ammonia aomoriensi	28	100.0	11	100.0	85	100.0	2072	100.0	93	100.0	11	100.0		
	Elphidium excavatum excavatu														
	Elphidium excavatum clavatum														
	Elphidium incertum														
	Total number of calcareous individuals	28		11		85		2072		93		11			
	Reophax dentaliniformi														
	Total number of agglutinated individuals														
	Total number of living specimens	28		11		85		2072		93		11			
	Species number														
	Sediment volume (cm^3)	15.		15.		15.		15.		15.		15.			
	Population density (ind. $10\,cm^{-3}$)	189.3		75.		562.8		1362.		612.8		77.			
1865_C	Species														
	Ammonia aomoriensi	87	100.0	10	100.0	45	100.0	2121	100.0	1402	100.0	21	100.0	62	100.0
	Elphidium excavatum excavatu														
	Elphidium excavatum clavatum														
	Elphidium gerthi														
	Elphidium incertum														
	Total number of calcareous individuals	87		10		45		2121		1402		21		62	
	Ammotium cassi														
	Reophax dentaliniformi														
	Total number of agglutinated individuals														
	Total number of living specimens	87		10		45		2121		1402		21		62	
	Species number														
	Sediment volume (cm^3)	15.		15.		15.		15.		15.		15.		15.	
	Population density (ind. $10\,cm^{-3}$)	572.0		71.		300.5		1394.		921.8		142.7		410.9	

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Table 2. Continued.

pCO_2-treatment	Living foraminiferal species > 63 µm	Months Jun	%	Jul	%	Aug	%	Sep	%	Oct	%	Nov	%	Dec	%
3247_A	Species														
	Ammonia aomoriensi	85	100.0	37	94.	47	100.0	59	100.0	70	100.0	84	100.0	43	100.0
	Elphidium excavatum excavatu				0.8										
	Elphidium excavatum clavatum														
	Elphidium incertum			18	4.5										
	Total number of calcareous individuals	85		39		47		59		70		84		43	
	Reophax dentaliniformi														
	Total number of agglutinated individuals														
	Total number of living specimens	85		39		47		59		70		84		43	
	Species number														
	Sediment volume (cm^3)	15.		15.		15.		15.		15.		15.		15.	
	Population density (ind. $10\,cm^{-3}$)	558.8		260.4		312.3		388.6		462.9		555.6		286.0	
3247_B	Species														
	Ammonia aomoriensi	1173	100.0	17	82.	22	100.0	38	100.0	70	100.0	1416	100.0	37	100.0
	Elphidium excavatum excavatu				0.5										
	Elphidium excavatum clavatum				0.9										
	Elphidium incertum			35	16.										
	Total number of calcareous individuals	1173		21		22		38		70		1416		37	
	Reophax dentaliniformi				0.5										
	Total number of agglutinated individuals														
	Total number of living specimens	1173		21		22		38		70		1416		37	
	Species number														
	Sediment volume (cm^3)	15.		15.		15.		15.		15.		15.		15.	
	Population density (ind. $10\,cm^{-3}$)	771.2		142.7		146.0		252.5		461.5		931.0		243.3	
3247_C	Species														
	Ammonia aomoriensi	63	100.0	31	93.	42	100.0	1388	100.0	64	100.0	48	100.0		
	Elphidium excavatum excavatu				0.6										
	Elphidium excavatum clavatum				0.3										
	Elphidium incertum			18	5.4										
	Total number of calcareous individuals	63		33		42		1388		64		48			
	Reophax dentaliniformi														
	Total number of agglutinated individuals														
	Total number of living specimens	63		33		42		1388		64		48			
	Species number														
	Sediment volume (cm^3)	15.		15.		15.		15.		15.		15.			
	Population density (ind. $10\,cm^{-3}$)	418.1		218.3		282.1		912.6		422.1		318.2			

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Table 3. List of dead foraminifera collected from each culture vessel during six month incubation time, size fraction 63–2000 µm.

pCO_2-treatment	Dead foraminiferal species > 63 µm	Months Jun	%	Jul	%	Aug	%	Sep	%	Oct	%	Nov	%	Dec	%
430_A	Species														
	Ammonia aomoriensis	20	76.9	71	74.0	25	52.1	192	90.6	325	91.5	158	83.6	107	89.2
	Elphidium excavatum excavatum			4	4.2			1	0.5			16	8.5	1	0.8
	Elphidium excavatum clavatum	3	11.5			1	2.1							1	0.8
	Elphidium incertum	2	7.7	17	17.7	18	37.5	13	6.1	19	5.4	11	5.8	9	7.5
	Total number of calcareous individuals	25		92		44		206		344		185		118	
	Reophax dentaliniformis	1	3.8	4	4.2	4	8.3	6	2.8	11	3.1	4	2.1	2	1.7
	Total number of agglutinated individuals	1		4		4		6		11		4		2	
	Total number of individuals	26		96		48		212		355		189		120	
	Total number of species	4		4		4		4		3		4		5	
	Sediment volume (cm^3)	15.2		15.2		15.2		15.2		15.2		15.2		15.2	
	Abundance (tests 10 cm^{-3})	17.1		63.1		31.6		139.4		233.4		124.3		78.9	
430_B	Species														
	Ammonia aomoriensis	61	87.1	84	74.3	39	68.4	199	91.7	127	88.2	125	76.7	127	83.6
	Elphidium excavatum excavatum			3	2.7	1	1.8	1	0.5			9	5.5	4	2.6
	Elphidium excavatum clavatum	1	1.4									3	1.8		
	Elphidium incertum	6	8.6	21	18.6	13	22.8	13	6.0	14	9.7	18	11.0	17	11.2
	Total number of calcareous individuals	68		108		53		213		141		155		148	
	Reophax dentaliniformis	2	2.9	5	4.4	4	7.0	4	1.8	3	2.1	8	4.9	4	2.6
	Total number of agglutinated individuals	2		5		4		4		3		8		4	
	Total number of individuals	70		113		57		217		144		163		152	
	Total number of species	4		4		4		4		3		5		4	
	Sediment volume (cm^3)	15.2		15.2		15.2		15.2		15.2		15.2		15.2	
	Abundance (tests 10 cm^{-3})	46.0		74.3		37.5		142.7		94.7		107.2		99.9	
430_C	Species														
	Ammonia aomoriensis	30	83.3	73	68.9	263	92.0			284	92.2	185	83.3		
	Elphidium excavatum excavatum					3	1.0			3	1.0	11	5.0		
	Elphidium excavatum clavatum	2	5.6												
	Elphidium incertum	3	8.3	25	23.6	15	5.2			18	5.8	21	9.5		
	Total number of calcareous individuals	35		98		281				305		217			
	Reophax dentaliniformis	1	2.8	8	7.5	5	1.7			3	1.0	5	2.3		
	Total number of agglutinated individuals	1		8		5				3		5			
	Total number of individuals	36		106		286				308		222			
	Total number of species	4		3		4				4		4			
	Sediment volume (cm^3)	15.2		15.2		15.2				15.2		15.2			
	Abundance (tests 10 cm^{-3})	23.7		69.7		188.0				202.5		146.0			

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Table 3. Continued.

pCO_2-treatment	Dead foraminiferal species > 63 µm	Months Jun	%	Jul	%	Aug	%	Sep	%	Oct	%	Nov	%	Dec	%
907_A	Species														
	Ammonia aomoriensis	135	94.4	96	84.2	30	75.0	133	92.4	247	95.4	318	91.4	227	88.3
	Elphidium excavatum excavatum	1	0.7	2	1.8	3	7.5	1	0.7	2	0.8	6	1.7	2	0.8
	Elphidium excavatum clavatum	3	2.1	1	0.9			1	0.7	1	0.4	2	0.6		
	Elphidium incertum	2	1.4	9	7.9	7	17.5	9	6.3	4	1.5	10	2.9	6	2.3
	Total number of calcareous individuals	141		108		40		144		254		336		235	
	Reophax dentaliniformis	2	1.4	6	5.3					5	1.9	12	3.4	22	8.6
	Total number of agglutinated individuals	2		6		0		0		5		12		22	
	Total number of individuals	143		114		40		144		259		348		257	
	Total number of species	5		5		3		4		5		5		4	
	Sediment volume (cm^3)	15.2		15.2		15.2		15.2		15.2		15.2		15.2	
	Abundance (tests 10 cm^{-3})	94.0		75.0		26.3		94.7		170.3		228.8		169.0	
907_B	Species														
	Ammonia aomoriensis	19	70.4	78	90.7	141	93.4	176	95.1			289	94.1	196	91.6
	Elphidium excavatum excavatum	1	3.7	1	1.2	2	1.3	5	2.7			4	1.3	2	0.9
	Elphidium excavatum clavatum	2	7.4					1	0.5					1	0.5
	Elphidium incertum	3	11.1	5	5.8	7	4.6	3	1.6			10	3.3	3	1.4
	Total number of calcareous individuals	25		84		150		185				303		202	
	Armorella sphaerica													4	1.9
	Reophax dentaliniformis	2	7.4	2	2.3	1	0.7					4	1.3	8	3.7
	Total number of agglutinated individuals	2		2		1		0				4		12	
	Total number of individuals	27		86		151		185				307		214	
	Total number of species	5		4		4		4				4		6	
	Sediment volume (cm^3)	15.2		15.2		15.2		15.2				15.2		15.2	
	Abundance (tests 10 cm^{-3})	17.8		56.5		99.3		121.6				201.8		140.7	
907_C	Species														
	Ammonia aomoriensis	28	73.7	63	88.7	143	94.1	276	93.6	324	94.5	323	89.0		
	Elphidium excavatum excavatum			2	2.8	3	2.0	8	2.7	4	1.2	18	5.0		
	Elphidium excavatum clavatum	4	10.5	2	2.8			1	0.3	1	0.3	3	0.8		
	Elphidium incertum	6	15.8	2	2.8	6	3.9	5	1.7	4	1.2	11	3.0		
	Total number of calcareous individuals	38		69		152		290		333		355			
	Reophax dentaliniformis			2	2.8			5	1.7	10	2.9	8	2.2		
	Total number of agglutinated individuals	0		2		0		5		10		8			
	Total number of individuals	38		71		152		295		343		363			
	Total number of species	3		5		3		5		5		5			
	Sediment volume (cm^3)	15.2		15.2		15.2		15.2		15.2		15.2			
	Abundance (tests 10 cm^{-3})	25.0		46.7		99.9		194.0		225.5		238.7			

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Table 3. Continued.

pCO_2-treatment	Dead foraminiferal species > 63 µm	Months Jun	%	Jul	%	Aug	%	Sep	%	Oct	%	Nov	%	Dec	%
1865_A	Species														
	Ammonia aomoriensis	42	68.9	85	86.7	78	82.1			43	91.5	206	83.7	260	94.2
	Elphidium excavatum excavatum	3	4.9			10	10.5			3	6.4	9	3.7		
	Elphidium excavatum clavatum	7	11.5	1	1.0	1	1.1					2	0.8		
	Elphidium incertum	7	11.5	4	4.1	5	5.3					28	11.4	3	1.1
	Total number of calcareous individuals	59		90		94				46		245		263	
	Ammotium cassis					1	1.1								
	Reophax dentaliniformis	2	3.3	8	8.2					1	2.1	1	0.4	13	4.7
	Total number of agglutinated individuals	2		8		1				1		1		13	
	Total number of individuals	61		98		95				47		246		276	
	Total number of species	5		4		5				3		5		3	
	Sediment volume (cm^3)	15.2		15.2		15.2				15.2		15.2		15.2	
	Abundance (tests $10\,cm^{-3}$)	40.1		64.4		62.5				30.9		161.7		181.5	
1865_B	Species														
	Ammonia aomoriensis	48	72.7	50	84.7	44	83.0	37	86.0	56	93.3	136	83.4		
	Elphidium excavatum excavatum	1	1.5			5	9.4	5	11.6	1	1.7	8	4.9		
	Elphidium excavatum clavatum	3	4.5							1	1.7				
	Elphidium incertum	14	21.2	1	1.7							13	8.0		
	Total number of calcareous individuals	66		51		49		42		58		157			
	Reophax dentaliniformis			8	13.6	4	7.5	1	2.3	2	3.3	6	3.7		
	Total number of agglutinated individuals	0		8		4		1		2		6			
	Total number of individuals	66		59		53		43		60		163			
	Total number of species	4		3		3		3		4		4			
	Sediment volume (cm^3)	15.2		15.2		15.2		15.2		15.2		15.2			
	Abundance (tests $10\,cm^{-3}$)	43.4		38.8		34.8		28.3		39.4		107.2			
1865_C	Species														
	Ammonia aomoriensis	33	67.3	52	91.2	45	91.8	78	90.7	41	93.2	211	92.1	205	93.2
	Elphidium excavatum excavatum	4	8.2	1	1.8	3	6.1	5	5.8	1	2.3	5	2.2	1	0.5
	Elphidium excavatum clavatum	5	10.2					1	1.2	2	4.5				
	Elphidium gerthi	1	2.0												
	Elphidium incertum	4	8.2	2	3.5	1	2.0	1	1.2			5	2.2	2	0.9
	Total number of calcareous individuals	47		55		49		85		44		221		208	
	Ammotium cassis													1	0.5
	Reophax dentaliniformis	2	4.1	2	3.5			1	1.2			8	3.5	11	5.0
	Total number of agglutinated individuals	2		2		0		1		0		8		12	
	Total number of individuals	49		57		49		86		44		229		220	
	Total number of species	6		4		3		5		3		4		5	
	Sediment volume (cm^3)	15.2		15.2		15.2		15.2		15.2		15.2		15.2	
	Abundance (tests $10\,cm^{-3}$)	32.2		37.5		32.2		56.5		28.9		150.6		144.6	

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Table 3. Continued.

pCO_2-treatment	Dead foraminiferal species > 63 µm	Months Jun	%	Jul	%	Aug	%	Sep	%	Oct	%	Nov	%	Dec	%
3247_A	Species														
	Ammonia aomoriensis	41	75.9	45	68.2	109	86.5	85	86.7	75	90.4	70	88.6	39	84.8
	Elphidium excavatum excavatum	3	5.6	1	1.5	3	2.4	1	1.0	1	1.2	2	2.5		
	Elphidium excavatum clavatum	3	5.6			2	1.6			1	1.2				
	Elphidium incertum	6	11.1	17	25.8	12	9.5	9	9.2	4	4.8	5	6.3	1	2.2
	Total number of calcareous individuals	53		63		126		95		81		77		40	
	Reophax dentaliniformis	1	1.9	3	4.5			3	3.1	2	2.4	2	2.5	6	13.0
	Total number of agglutinated individuals	1		3		0		3		2		2		6	
	Total number of individuals	54		66		126		98		83		79		46	
	Total number of species	5		4		4		4		5		4		3	
	Sediment volume (cm^3)	15.2		15.2		15.2		15.2		15.2		15.2		15.2	
	Abundance (tests $10\,cm^{-3}$)	35.5		43.4		82.8		64.4		54.6		51.9		30.2	
3247_B	Species														
	Ammonia aomoriensis	80	85.1	101	80.8	70	86.4	88	83.0	100	84.7	40	83.3	59	86.8
	Elphidium excavatum excavatum	2	2.1	1	0.8	1	1.2	2	1.9	1	0.8	1	2.1		
	Elphidium excavatum clavatum	6	6.4	2	1.6					1	0.8				
	Elphidium incertum	5	5.3	15	12.0	6	7.4	8	7.5	14	11.9	4	8.3	4	5.9
	Total number of calcareous individuals	93		119		77		98		116		45		63	
	Reophax dentaliniformis	1	1.1	6	4.8	4	4.9	8	7.5	2	1.7	3	6.3	5	7.4
	Total number of agglutinated individuals	1		6		4		8		2		3		5	
	Total number of individuals	94		125		81		106		118		48		68	
	Total number of species	5		5		4		4		5		4		3	
	Sediment volume (cm^3)	15.2		15.2		15.2		15.2		15.2		15.2		15.2	
	Abundance (tests $10\,cm^{-3}$)	61.8		82.2		53.3		69.7		77.6		31.6		44.7	
3247_C	Species														
	Ammonia aomoriensis	156	92.9	103	83.1	84	85.7	74	83.1	128	92.8	54	90.0		
	Elphidium excavatum excavatum	3	1.8	11	8.9	4	4.1	3	3.4			1	1.7		
	Elphidium excavatum clavatum	4	2.4			1	1.0								
	Elphidium incertum	4	2.4	8	6.5	9	9.2	6	6.7	6	4.3	4	6.7		
	Total number of calcareous individuals	167		122		98		83		134		59			
	Reophax dentaliniformis	1	0.6	2	1.6			6	6.7	4	2.9	1	1.7		
	Total number of agglutinated individuals	1		2		0		6		4		1			
	Total number of individuals	168		124		98		89		138		60			
	Total number of species	5		4		4		4		3		4			
	Sediment volume (cm^3)	15.2		15.2		15.2		15.2		15.2		15.2			
	Abundance (tests $10\,cm^{-3}$)	110.5		81.5		64.4		58.5		90.7		39.4			

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Table 4. Two-way analysis of variance (ANOVA) revealed the effect of pCO_2 and incubation time on test diameter of *A. aomoriensis*. Significant results are represented in bold. SS = Sum of Squares, d.f. = degrees of freedom, MS = Mean Squares.

Test diameter of living *A. aomoriensi* Factor	SS	d.f.	MS	*F*	*p*
pCO_2	1213.0	3.0	404.0	0.61	0.6100
Incubation time	59 800.0	5.0	12 000.0	**18.14**	**0.000**
pCO_2 × time	21 200.0	15.0	1412.0	**2.14**	**0.025**
Test diameter of dead *A. aomoriensi* Factor	**SS**	**d.f.**	**MS**	***F***	***p***
pCO_2	7351.0	3.0	2450.0	2.46	0.0750
Incubation time	83 000.0	5.0	16 600.0	**16.65**	**0.000**
pCO_2 × time	21 800.0	15.0	1450.0	1.45	0.1630

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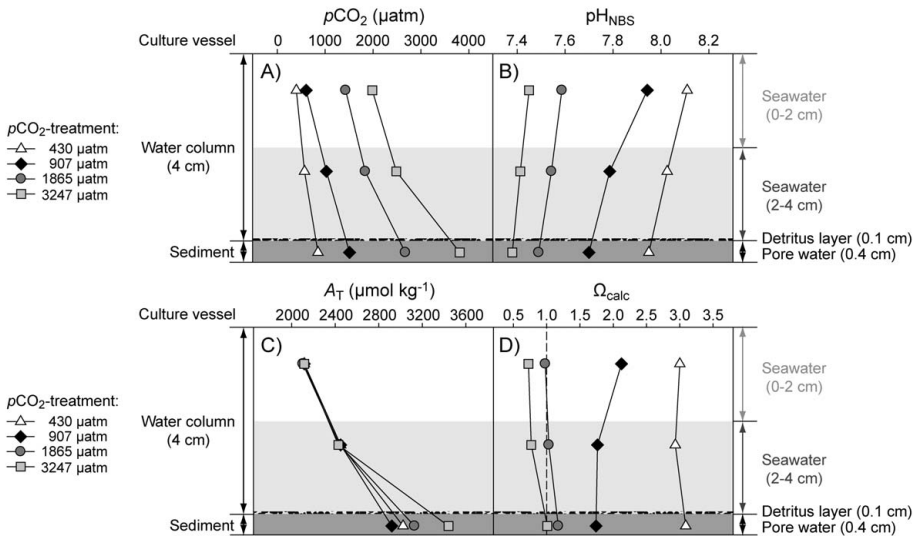

Fig. 1. Gradient of carbonate chemistry parameters of **(A)** partial pressure of CO_2 (pCO_2), **(B)** pH_{NBS}, **(C)** total alkalinity (A_T) and **(D)** saturation state of calcite (Ω_{calc}) in the seawater and sediment pore water for 4 pCO_2-treatments after six months incubation time.

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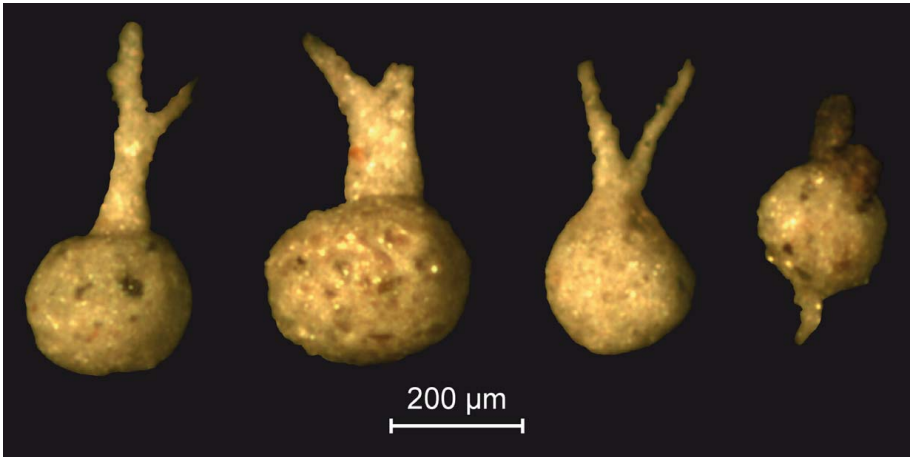

Fig. 2. Light micrograph images of the arenaceous species *Armorella sphaerica*.

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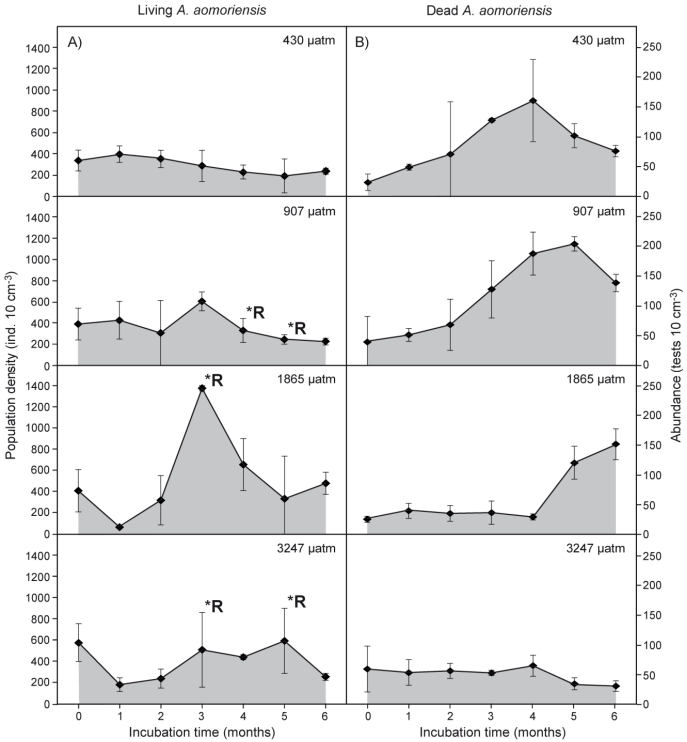

Fig. 3. (A) Population density and **(B)** abundance of living and dead *A. aomoriensis* at 4 pCO_2-levels during six months incubation time. The symbols represent the mean in three replicates (mean ± standard deviation). Reproduction events are indicated by asterisk and bold R.

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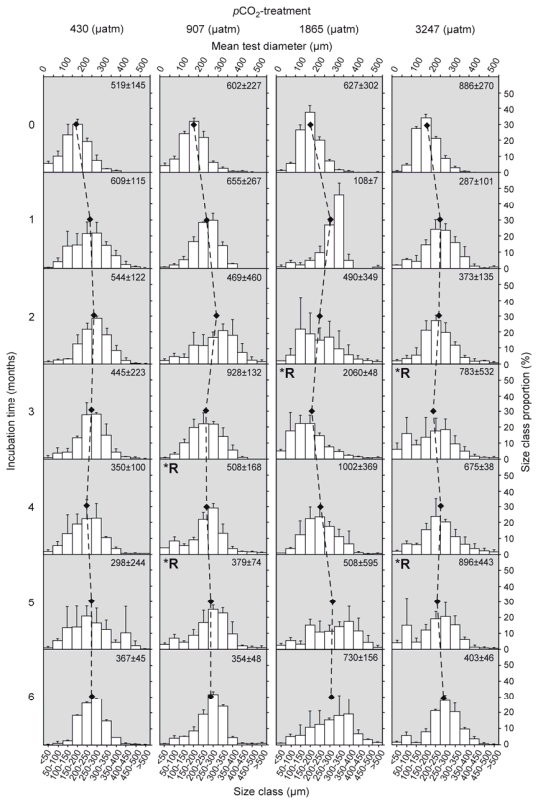

Fig. 4. Histogram of size class proportions of living *A. aomoriensis* during six months incubation. Light grey bars represent relative proportion of 11 size classes ranging from < 50 until > 500 µm in 50 µm intervals. Mean test diameter is displayed by the black diamonds and dashed lines. The number in each figure represents the number of individuals (mean ± standard deviation of three replicates). Reproduction events are indicated by asterisk and bold R.

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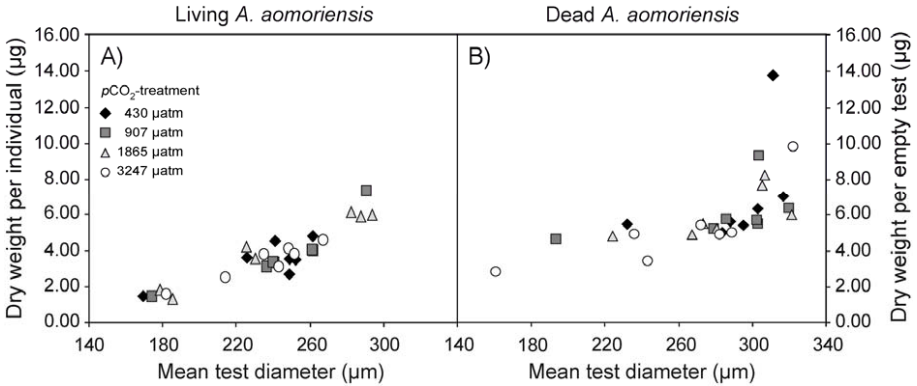

Fig. 5. Total dry weight of **(A)** living specimensincluding cytoplasm and **(B)** empty test of *A. aomoriensis* in relation to mean test diameter for the 4 tested pCO_2-treatments.

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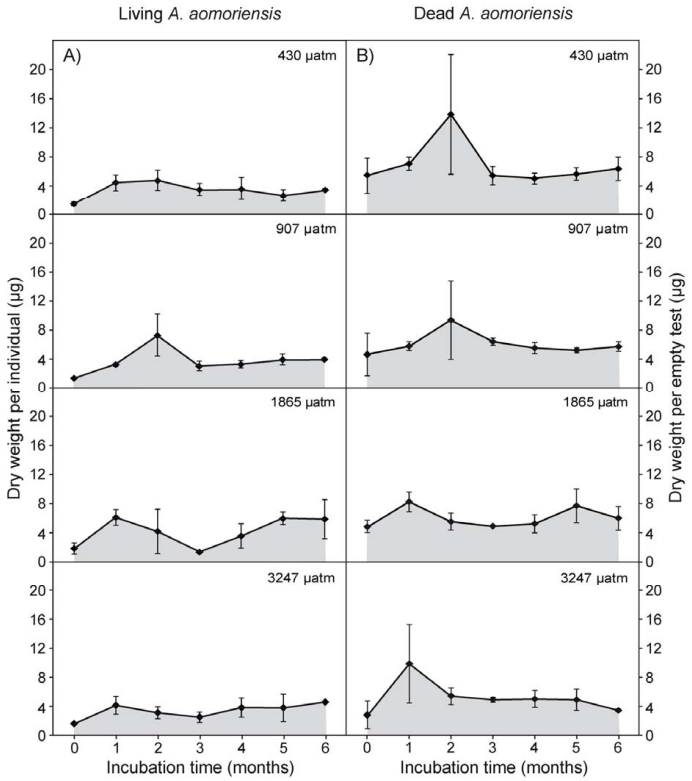

Fig. 6. Mean dry weight per individual including cytoplasm/empty test and standard deviation of three replicates of **(A)** living and **(B)** dead *A. aomoriensis* of the 4 tested pCO_2-levels during six months incubation.

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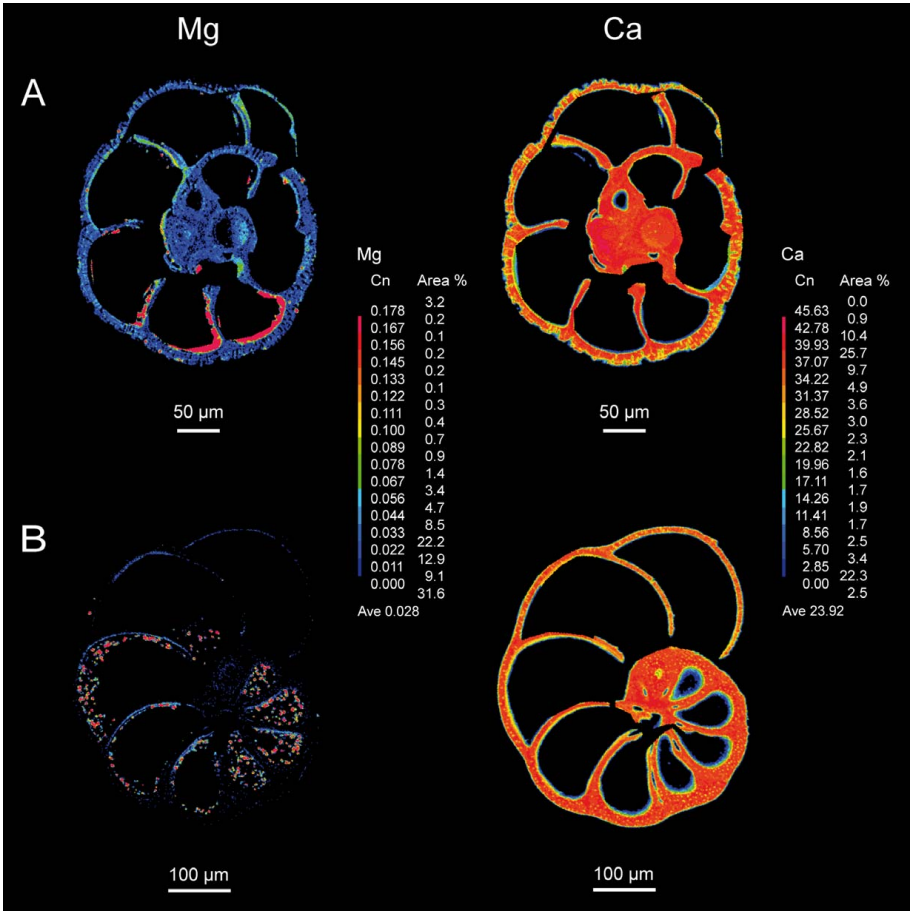

Fig. 7. EMP maps of Mg and Ca of test cross-sections from cultured **(A)** living *A. aomoriensis* and **(B)** living *E. incertum*. All intensity values are expressed in counts per second (cps) as shown in the color bars.

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