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Experimental study on the effect of salinity on growth rates of Arctic-sea-ice algae from the Greenland Sea

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An Arctic bottom ice algal community collected from a pack ice floe in the Greenland Sea in autumn 1995 was cultured at 10 salinities ranging from 4.0 to 90.8 PSU for 19 days. Growth of species was determined by microscopical analysis of samples taken every 3 to 5 days. During the experiment the abundance of the algae increased over a wide salinity range from 4.0 to 74.0 PSU, but decreased at the highest salinity (90.8). Maximum growth rates were 0.29 d^{-1} for the entire ice algal community and 0.42 d^{-1} for individual taxa. The final composition of the algal communities varied with salinities. Phytoflagellates and *Chaetoceros* spp. were most abundant at low salinities (≤ 12.2), while pennate diatoms of the genus *Nitzschia* were the dominant algae at higher salinities.

Introduction

Arctic sea ice covers an area of 14×10^6 km^2 at maximum and is the realm of a diverse community of organism (Horner 1985). Environmental conditions inside the sea ice exhibit strong seasonal fluctuations (Eicken 1992). In winter, almost no light is available and ice temperatures may drop to below –10 °C, while in summer there is continuous light and ice temperatures near 0 °C. Changes in ice temperatures in the observed range of at least ±10 °C, affect the ice biota in two major ways. Firstly, physiological processes within the cells are temperature dependent and modify e.g., respiration and primary production rates to different degrees (Pomeroy & Deibel 1986, Tilzer & Dubinsky 1987). Secondly, changes of ice temperature automatically alter the brine salinity (Assur 1958) and therefore the osmotic stress on ice organisms. Low ice temperatures are linked to high brine salinities and *vice versa*. When the temperature decreases to e.g., –10 °C in winter, brine salinity rises to 143 PSU, which is approximately 4–5 times higher than normal sea water salinity. In summer fresh water melt ponds form on the surface of Arctic ice floes with salinities often close to 0. Accumulation of fresh water may also occur at the underside of ice floes (Eicken

1994, Gradinger 1996), exposing algae of the bottom ice community to low salinities. Further, brine salinity exhibits strong vertical gradients in the ice (Eicken 1992). As a result, the biota of Arctic sea ice must cope with enormous salinity fluctuations, which may affect the composition and distribution of algal communities within the ice as was seen in first-year ice of the Hudson Bay, Arctic Canada (Poulin *et al*. 1983). Consequently, our experiments were conducted to study the effects of salinity variation on algal growth rates of natural communities.

Previous studies with species isolated from Arctic and Antarctic sea ice indicated their wide adaptability to changing salinities. Four Arctic ice diatom species collected in spring in the Chukchi and Beaufort Seas were relatively euryhaline and maintained growth rates of 0.6 to 0.8 divisions per day over a salinity range of 10 to 50 PSU (Grant & Horner 1976). For Antarctic ice algal species growth occurred at temperatures down to –5.5 °C and a corresponding salinity of 95 PSU (Bartsch 1989). At lower temperatures (–7.5 °C) and higher salinities (150 PSU) no increases in abundance were observed but cells remained viable. Freshly collected bottom ice algal communities behaved similarily growing at salinities from 11.5 PSU to 34 PSU and growth rates increasing with increasing salinity (Vargo *et al*. 1986). High temperature and salinity tolerance exists not only for ice algal taxa but also for protozoans (Spindler 1996) and metazoans (Dahms *et al*. 1990, Friedrich 1997, Gradinger & Schnack-Schiel 1998).

Earlier Arctic studies were conducted with species isolated from first-year ice close to coastal areas in spring and summer and focused on growth of ice algae when salinity was either increased or decreased. The objective of our investigation was to determine salinity effects on a natural ice algal community and selected species growing within that community. Our samples were collected from drifting pack ice in the East Greenland Current in autumn when algal populations face drastic changes in their environment. We measured growth rates by microscopic observations over a period of nearly three weeks to determine (1) the salinity range over which Arctic ice algae are able to survive, and (2) whether certain algal taxa are favored by either salinity increase or decrease.

Materials and methods

The experiment was carried out onboard the German research vessel *Polarstern* during the ARKTIS-XI/2 expedition (Krause 1996) to the Greenland Sea (September–October 1995). All sampling took place at three stations: 79°59´N, 4°14´W (for ice cores), and 80°10´N, 6°00´W, and 80°31´N, 9°51´W (for surface water). Ice cores were collected with a 10 cm diameter ice corer. Salinities were measured with a WTW LF196 coprocessor conductivity meter.

Salinities between 1 and 100 PSU (Table 1) were achieved by mixing different fractions of high saline brine and low saline melt water (LSMW). The brine solution (124.5 PSU) was obtained by freezing 0.2 µm-filtered surface sea water (32.5 PSU) from the Greenland Sea at –30 °C and subsequent collection of draining brine

Table 1. Ranges of achieved salinities (PSU) for the cultures of ice algae in the experiment. Initial salinity of the melted ice was 25.7 PSU.

Salinity 1: before addition of melted ice	Salinity 2 (S_2): after addition of melted ice	Salinity difference: S_2–25.7
1.1	4.0	–21.7
10.5	12.2	–13.5
19.9	20.6	–5.1
32.5	31.9	6.2
39.9	38.4	12.7
50.0	47.4	21.7
59.8	56.0	30.3
70.6	65.6	39.9
80.3	74.0	48.3
100.2	90.8	65.1

at 0 °C. For the LSMW, the top 10 cm segments of two ice cores taken from an ice floe were melted and filtered through 0.2 µm Nuclepore filter. The resulting salinity was 1.1 PSU.

The bottom 1.5 cm segments of two ice cores were melted in 400 ml 0.2 µm-filtered seawater to avoid osmotic damage of the ice organisms (Garrison & Buck 1986). Potential grazers were removed by filtration through 64 µm gauze. The final salinity of the melted ice was 25.7 PSU. Fifty ml of the melted ice were added to 400 ml of water with different salinities and the final salinity was determined (Table 1). Each salinity treatment was divided into two 250 ml Corner polystyrene tissue culture vials and incubated at an irradiance of 47.5 µmol m^{-2} s^{-1} (8h L:16h D) and a temperature of 1 ± 1 °C. No nutrients were added. The vials were gently shaken 3 times each day.

Subsamples (25 ml) were taken from each vial 1, 3, 6, 9, 14 and 19 days after the start of the experiment and were fixed with borax-buffered formalin (1% final concentration). Algal species composition and abundances were determined according to HELCOM (1988) using a Zeiss Axiovert 135 inverted light microscope with phase contrast illumination. For cell counts two 15 ml subsamples from each of the two vials with identical salinities were pooled and than counted. Species were identified based on Medlin and Priddle (1990).

Algal growth rate μ_t was calculated:

$$\mu_t = (\ln N_{t2} - \ln N_{t1})/(t_2 - t_1) \quad (1)$$

with N_{t1} and N_{t2} representing cell abundances (cells ml^{-1}) at time t_1 and t_2, respectively.

Salinity was measured again at the end of the experiment, and no changes were found compared to the initial values.

Results

The ice algal community used for the experiment was dominated by diatoms. The initial algal abundance was 265 cells ml^{-1} (Fig. 1) with *Nitzschia arctica* (62%), *Nitzschia longissima* (10%), *Hantzschia weyprechtii* (8%) and *Nitzschia frigida* (7%) (Table 2) being the main taxa.

Species abundance and composition changed differently with time at the various salinities. Cell density increased in nearly all cultures except for the highest salinity of 90.8, where a slight decrease occurred (Fig. 1). In nearly all other treatments, algal growth rates exceeded values of 0.10 d^{-1} for at least part of the experiment (Table 3). Highest abundances with values above 4×10^6 cells ml^{-1} were reached at medium salinities of 12.2 PSU to 20.6 PSU after 19 days. During the last 5 days of the experiment growth rates were often reduced or negative.

Fig. 2 shows the relative composition of the algal community for each sampling day and salinity. During the first 6 days, *Nitzschia arctica* dominated at all salinities. After 14 days (Table 2), *N. arctica* was the most abundant species only at salinities $S \geq 31.9$ PSU. Dominant taxa at other salinities were phytoflagellates (4.0 PSU), *Chaetoceros* spp. (12.2 PSU) and *Nitzschia pseudodelicatissima* (20.6 PSU). Consequently

Table 2. Relative contribution (%) of algal taxa to total abundance at day 0 and day 14 of the experiment. Dominant taxa for each salinity (S; PSU) are in bold.

Taxa	Day 0	Day 14									
		S = 4.0	12.2	20.6	31.9	38.4	47.4	56.0	65.6	74.0	90.8
Chaetoceros spp.	0.5	21.1	**41.7**	8.3	6.1	8.2	4.5	4.5	1.3	2.5	1.6
Hantzschia weyprechtii	8.3	0.0	0.2	1.1	9.5	1.6	4.5	8.5	7.0	9.2	18.5
Nitzschia arctica	**62.0**	1.6	4.7	14.7	**32.0**	**24.5**	**32.8**	**36.2**	**50.3**	**45.4**	**39.0**
Nitzschia closterium	4.8	1.6	0.7	0.8	10.2	16.3	12.6	10.3	5.7	4.2	4.4
Nitzschia cylindrus	0.2	5.5	5.0	3.6	12.9	5.4	9.3	5.4	10.8	7.6	5.2
Nitzschia frigida	7.1	1.6	1.4	2.8	6.1	4.3	6.1	4.0	6.4	10.9	4.4
Nitzschia longissima	9.8	0.0	0.5	0.0	2.0	1.1	1.2	0.4	1.9	0.0	2.0
Nitzschia pseudodelicatissima	2.3	7.0	23.3	**47.9**	4.8	18.5	11.7	6.3	1.3	5.0	7.2
Nitschia pseudonana	0.0	0.0	1.7	0.0	6.8	6.5	10.9	10.7	5.1	6.7	13.7
Phytoflagellates	0.0	**55.5**	16.7	10.4	0.7	2.7	0.8	0.9	0.0	0.0	0.0
Other diatom taxa	5.0	6.3	4.0	10.4	8.8	10.9	5.7	12.9	10.2	8.4	4.0

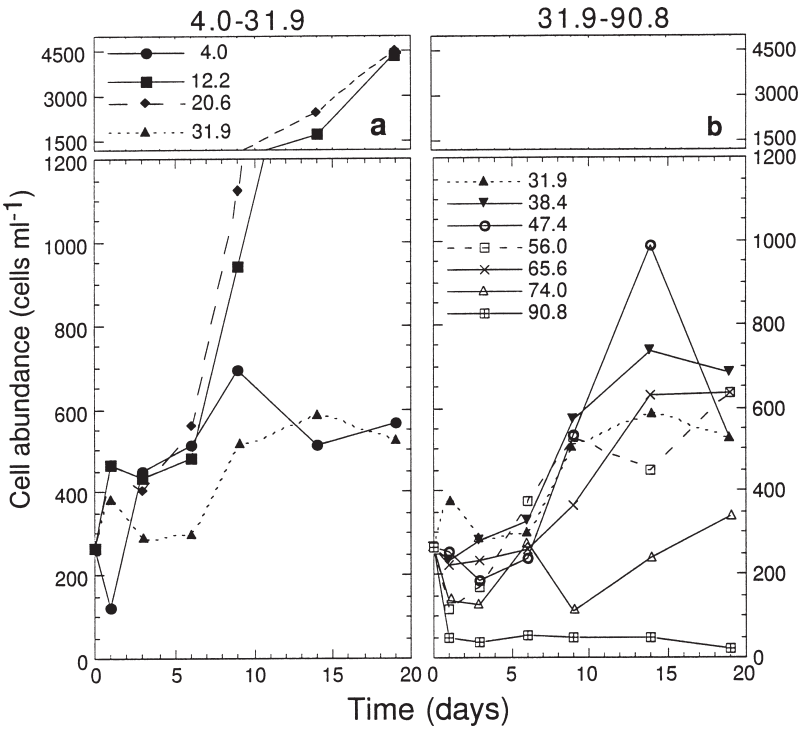

Fig. 1. Growth of ice algal community at different salinites: a) 4.0 to 31.9 PSU, b) 31.9 to 90.8 PSU.

the salinity specific growth response was highly species dependent (Fig. 3).

Chaetoceros spp. grew at a rate above 0.10 d^{-1} over a wide range of salinities (S = 4.0–74.0 PSU) with maximum increase at S = 12.2 PSU. The two most abundant pennate species (*Nitzschia arctica* and *Nitzschia pseudodelicatissima*) also exhibited growth over a wide range of salinites. *N. arctica* was sensitive to reduced salinities ($S \leq 12.2$ PSU) reacting with decreased abundance, and showing relatively low but constant growth rates of about 0.05 d^{-1} over a salinity range from 20.6 to 74.0. *N. pseudodelicatissima* was capable of faster growth (μ_{max} = 0.28 at S = 20.6 PSU) than *N. arctica* at a salinity range from 4.0 PSU to 56.0 PSU, but at higher salinities growth of *N. pseudodelicatissima* ceased and abundances decreased. Phytoflagellates exhibited highest growth rates (μ_{max} = 0.42 d^{-1} at S = 4.0 PSU) at low salinities $S \leq 20.6$ PSU and were strongly affected by high salinities. Their abundance drastically decreased at salinities above 65.6 PSU (Table 2).

Table 3. The algal community growth rates (μ, day^{-1}) at different time periods of the experiment.

Salinity (PSU)	Time (days)					
	1–6	1–14	1–19	6–14	6–19	14–19
4.0	0.286	0.110	0.085	0.000	0.007	0.019
12.2	0.008	0.100	0.125	0.157	0.170	0.192
20.6	0.035	0.128	0.127	0.187	0.162	0.124
31.9	–0.049	0.033	0.017	0.084	0.043	–0.023
38.4	0.068	0.088	0.060	0.101	0.057	–0.015
47.4	–0.013	0.104	0.040	0.178	0.061	–0.127
56.0	0.232	0.103	0.094	0.023	0.041	0.070
65.6	0.030	0.080	0.058	0.111	0.069	0.003
74.0	0.139	0.042	0.050	–0.019	0.016	0.070
90.8	0.023	0.002	–0.045	–0.012	–0.072	–0.167

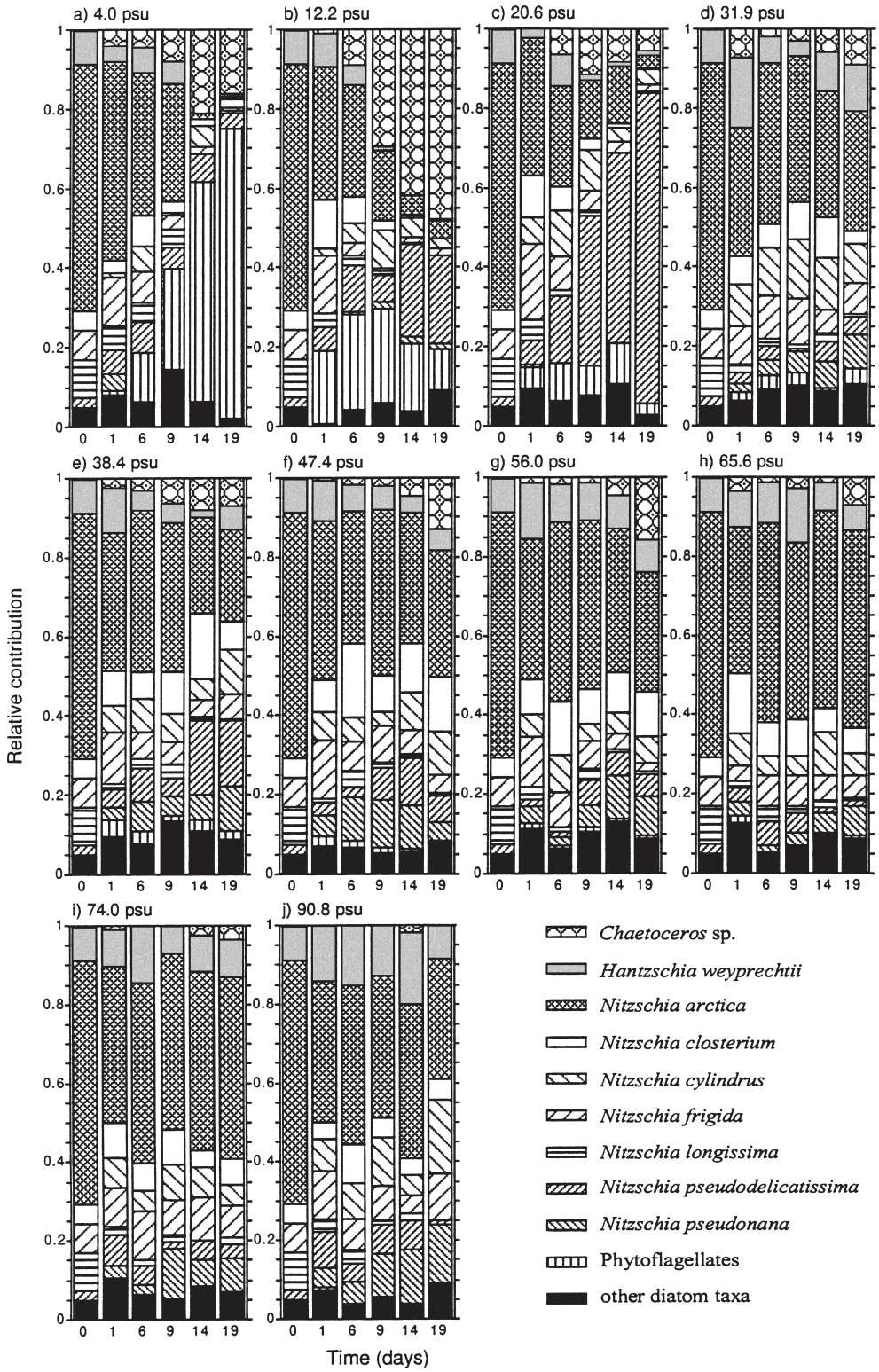

Fig. 2. Relative composition of the ice algal community at salinities from 4.0 to 90.8 PSU.

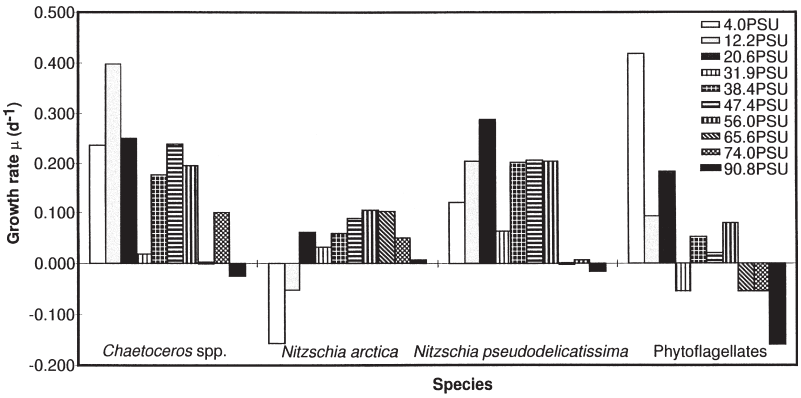

Fig. 3. Growth rates of different algal taxa during the first 14 days of the experiment in relation to salinity.

Discussion

Growth estimates of ice algal communities and single species kept in cultures vary between regions and seasons. In the Barents Sea, maximum growth rate for two cultured bottom ice diatom species was 0.8 d^{-1} (Hegseth 1992). Slower rates were reported for bottom ice microalgae from Hudson Bay with means of 0.06 to 0.13 d^{-1} (Maestrini *et al.* 1986), similiar to our data. *In situ* estimates of Arctic ice algal growth in spring revealed rates of 0.08 to 0.22 for diatoms (Gradinger *et al.* 1991). The observed growth rates for the Arctic pack ice community fall in a range typical for sea ice algae and should be regarded as minimum estimates for several reasons. Although we excluded larger grazers from our experiment by pre–screening, micrograzers such as heterotrophic flagellates and ciliates were also present in our samples. A total elimination of grazers from natural ice communities is not possible because many heterotrophic flagellates and ciliates are in the same size range as the algae. The ice treatment (melting in filtered sea water; dilution = 10) and the later salinity adjustment (dilution = 9) lead to a final organism concentration which was 90 times lower than in the original ice sample, and 450 times lower than in the brine channel network (20% of entire ice volume; data not shown) within the ice, respectively. The dilution causes a reduction of the grazing pressure (Landry & Hasset 1982) by a similar factor. Thus, we assume that grazing will not affect substantially the determined growth rates. A further artefact might be introduced by changing the nutrient regime, because the nutrient status varied between the different salinity treatments due to the mixture of varying amounts of melted ice cores and high saline brine at the beginning of the experiment. Nutrient concentrations inside the brine channels (NO_3 = 3.9 μmol l^{-1}; SiO_2 = 5.8 μmol l^{-1}; PO_4 = 0.3 μmol l^{-1}) were lower than the surface water values (NO_3 = 4–5 μmol l^{-1}; SiO_2 = 8–9 μmol l^{-1}; PO_4 = 0.7–1.0 μmol l^{-1}). Thus, the melting in surface water lead to an initial slight increase of nutrient availability for the ice algae. In the low salinity treatments, reduction of only the phosphate and nitrogen pool occurred by addition of the melted upper parts of ice floes (nutrient concentrations in the upper 20 cm of the ice floe: NO_3 = 0.0 μmol l^{-1}; SiO_2 = 8.2 μmol l^{-1}; PO_4 = 0.1 μmol l^{-1}), silicate concentrations remained constant. We conclude that the initial nutrient concentrations in the different salinity treatments did not cause the taxon specific growth differences, especially in the case of the phytoflagellate dominance at low salinities. The low growth rates of diatoms (e.g., *Nitzschia arctica*) at low salinities have to be attributed to a salinity effect. Besides these uncertainties, we chose our experimental approach because it simulates precisely the natural ongoing processes leading to salinity variations. Before the onset of ice melting, the salinity in brine channels and pockets within congelation ice ranges from above 150 PSU to 34 PSU (Grant & Horner 1976, Kottmeier & Sullivan 1988) depending on the ice temperature. During the summer, salinity may drop to near 0 PSU because of ice and snow melting at the surface of the ice floes and the subsequent formation of freshwater lenses (Grant & Horner 1976, Palmisano & Sullivan 1985, Grossi *et al.* 1987). These processes and the sources for salinity variations (surface melting vs. brine concentration) were simulated in our experiment by addition of brine or melted sea ice. Consequently, we assume that our results are simi-

lar to the naturally occurring growth reactions after salinity changes, including the changes of the nutrient availability, but without grazing impact.

Salinity tolerance and preference of ice algae show great variations. Antarctic sea ice algal communities, dominated by *Nitzschia stellata* and *Amphiprora* sp., grew faster at salinities of 30–50 PSU than at lower ones (Vargo *et al.* 1986, Arrigo & Sullivan 1992). In other studies, communities dominated by e.g., *Pleurosigma* sp., *Amphiprora kufferathii*, and *Pinnularia quadratarea* exhibited maximum growth rates at 6–10 PSU (Bunt 1964, Kottmeier & Sullivan 1988). In our study, *Chaetoceros* spp. grew fastest at a salinity of 12.2 PSU. Phytoflagellates reached their highest growth rates at 4.0 PSU, while pennate diatoms achieved fastest growth at higher salinities. All taxa were strongly inhibited at the highest salinity of our experiment (90.8 PSU), although cells remained intact and survived during the entire 19 days, which is similar to the observations of Bartsch (1989) for Antarctic ice diatoms. However, salinity tolerance may vary with time as ice algal communities adapt to their ambient salinity regime (Kottmeier & Sullivan 1988). We did not test for the combined effect of brine salinity and temperature on the ice organisms. Temperature *per se* affects the metabolism of organisms by altering firstly the reaction kinetics and secondly the membrane properties. Studies only on temperature induced growth changes demonstrated that most polar algae are psychrophilic (optimum < 15 °C) but maximum growth rates were obtained at temperatures (2–8 °C) above *in situ* values (< 0 °C) (Bunt 1968, Kottmeier & Sullivan 1988, Fiala & Oriol 1990). Thus, our data do not reflect optimum growth rates. A useful index to estimate temperature influences is the Q_{10} value. Photosynthesis responds to temperature changes with a Q_{10} of 1–6 (Palmisano *et al.* 1987, Kottmeier & Sullivan 1988, Arrigo & Sullivan 1992). The temperature responses of respiration are still unclear, and it is discussed that Q_{10} values for respiration are either lower (Bunt 1968, Sakshaug & Slagstad 1991, Tilzer & Dubinsky 1987) or equal (Robinson & le B. Williams 1993) to the photosynthetic Q_{10}. However, these changes are minor compared to the effect of salinity fluctuations (Bartsch 1989). In this study growth rates of Antarctic ice diatoms were nearly identical for several temperatures (ranging from –1 °C to equilibrium temperature as defined by Assur 1958) at each salinity step (e.g., salinity = 80 PSU; temperatures of –1 °C, –3.5 °C and –5.5 °C), demonstrating the overwhelming influence of salinity on growth characteristics.

Species-specific differences in the ability to acclimate to changes in salinity may cause shifts in species composition. Previous studies on salinity tolerance of sea ice organisms were mostly based on data from clonal cultures. Studies on the competition between species and the temporal evolution of the communities were absent (Horner 1985, Vargo *et al.* 1986, Bartsch 1989, Arrigo & Sullivan 1992, Spindler 1996). Our study demonstrates the strong influence of salinity on growth of Arctic ice algal species and changes in community composition. Brine salinity exhibits strong vertical gradients in sea ice (Eicken 1992) and, thus, contributes to the vertical stratification of algal communities in Arctic sea ice. The tolerance to low salinities may determine the survival of algae during the process of ice melting and their contribution to the seeding of marginal ice zone phytoplankton blooms.

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