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ON THE SALINITY TOLERANCE OF THE PLANKTONIC FORAMINIFER *NEOGLOBOQUADRINA PACHYDERMA* FROM ANTARCTIC SEA ICE

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Abstract: The sea ice of both of the Earth's polar regions contains an internal system of delicate brine channels and pockets which serve as a habitat for a variety of organisms including plants and animals. The large standing stock of algae in the ice provides an ample food source for heterotrophic consumers. The sea ice habitat is characterised by low temperatures and correspondingly high salinities. During winter, temperatures as low as −15℃ and salinities as high as 177 psu were recorded in the brine channel system of the upper part of Antarctic sea ice. The tolerance of sympagic organisms to increased salinities is remarkable. Algae grow in salinities of up to 95 psu and also sea ice animals can survive, grow and partly reproduce under high salinities. The foraminifer *Neogloboquadrina pachyderma* was subjected to a variety of different salinities. Formation of new chambers occurs in salinities of up to 58 psu, specimens survive 82 psu for at least a week, and drastic changes in salinity are tolerated, *e.g.* direct transfer from 30 to 60 psu or from 60 to 40 psu. Chamber formation rates are slightly slower at higher salinities and the final size of specimens decreases with increasing salinity. Reproduction was never observed in salinities above 50 psu, which corroborates earlier results that *N. pachyderma* does not reproduce within the sea ice.

1. Introduction

Sea ice from the Arctic and Antarctic regions contains an internal system of interconnected brine channels (WEISSENBERGER *et al.*, 1992). These are inhabited by a variety of smaller organisms including bacteria, different algal groups, fungi, protozoa and metazoa (HORNER, 1985) which are described as sympagic organisms (WHITAKER, 1977; HORNER *et al.*, 1992). This brine channel system develops during ice formation when fresh water crystals are formed and the rejected brine collects within the consolidating ice. Continuing freezing results in increasing salinity within the brine channel system, as more freshwater is incorporated into the growing ice. Temperatures within the ice environment and salinity within the brine channel system are correlated (ASSUR, 1960; MOREY *et al.*, 1984). At relatively modest low temperatures the salinity reaches high values (Table 1). Temperatures in the upper parts of the sea ice can fall below −15℃ with corresponding salinities of 177 psu during winter (BARTSCH, 1989). Thus, sympagic organisms have to cope with extreme conditions in regard to temperature and salinity compared to other organisms from the marine environment.

Responses to extreme salinities have been investigated for several sympagic organisms including diatoms from Arctic and Antarctic sea ice habitats (GRANT and HORNER,

Table 1. Temperature and salinity relationships within sea ice. After MOREY et al. (1984).

Temperature (°C)	−2	−4	−6	−8	−10	−12
Salinity (psu)	39.3	68.9	98.5	128.1	144.1	157.3

1976; VARGO *et al.*, 1986; KOTTMEIER and SULLIVAN, 1988; BARTSCH, 1989; ARRIGO and SULLIVAN, 1992), bacteria (ANONYMOUS, 1987), protozoans (LEE and FENCHEL, 1972), and crustaceans (AARSET and AUNAAS, 1987; DAHMS *et al.*, 1990; GRAINGER and MOHAMMED, 1990). Salinities as high as 145 psu were tolerated for six weeks by sympagic diatoms from the Antarctic pack-ice (BARTSCH, 1989), bacteria from the same environment were able to grow in seawater of 105 psu (ANONYMOUS, 1987), and a sympagic copepod from Weddell Sea fast-ice experienced mortality only above 90 psu (DAHMS *et al.*, 1990).

The planktonic foraminifer *Neogloboquadrina pachyderma* occurs predominantly in the polar oceans of both hemispheres. In southern latitudes it thrives in waters of relatively low salinities compared to other of the world's oceans (about 34 psu). Abundant *N. pachyderma*, however, are part of the sympagic community and live in pack and fast ice of the Southern Ocean (LIPPS and KREBS, 1974; SPINDLER and DIECKMANN, 1986; DIECKMANN *et al.*, 1991). Within the ice their concentration may exceed 1000 specimens l^{-1} in melted ice from certain portions of ice floes (DIECKMANN *et al.*, 1991). Foraminifers can be recovered alive by gentle extraction from the ice (see Section 2). There organisms actively move around, feed and grow by adding chambers to their tests when kept in culture dishes even when collection takes place during winter time. We therefore assume that *N. pachyderma* should be able to survive salinities above 50 psu and be active to some extent.

Salinity tolerances of planktonic foraminifers are rarely recorded. BIJMA *et al.* (1990) investigated the temperature and salinity ranges of 7 species of planktonic foraminifers from tropical to temperate regions. *Globigerinoides ruber* and *G. sacculifer* were the species which tolerated the highest salinities (49 and 47 psu respectively) followed by *Neogloboquadrina dutertrei* with an upper salinity limit of 46 psu. Salinity tolerances in planktonic foraminifers have been deduced from the fossil record. During the last glacial maximum (18 ka before present) the salinity of the Gulf of Aqaba was considerably higher than at present (about 41 psu) and exceeded 50 psu (REISS *et al.*, 1980). Although other groups of organisms (*e.g.* pteropods, coccolithophorids, benthic foraminifers) survived these conditions, planktonic foraminifers disappeared from the fossil record. This led WINTER *et al.* (1983) to conclude that 50 psu may be the upper limit for all planktonic foraminifers.

Neogloboquadrina pachyderma was found alive and active within the sea ice even during winter time (SPINDLER *et al.*, 1990). However, as dead foraminifers and empty shells also were found in upper parts of the ice (SPINDLER and DIECKMANN, 1986) it was of interest to investigate the salinity tolerances of this particular species.

2. Material and Methods

Specimens used in the experiments were collected during "POLARSTERN"-cruise ANT V/3 (September–December 1986) (SCHNACK-SCHIEL, 1987) from ice floes from the

inner Weddell Sea (Stations S10 and S19). For further details see SPINDLER *et al.* (1990). Ice cores were obtained using modified SIPRE ice corers and the organisms were subsequently extracted by melting the ice in large volumes of 0.2 μm filtered seawater to avoid osmotic stress (SPINDLER and DIECKMANN, 1986; GARRISON and BUCK, 1986). After extraction, the specimens were kept in petri dishes (diameter 10 cm) for two days in natural sea water (salinity 34 psu) at -1 °C before being directly transferred into plastic multi-well dishes (volume 12 cm^3 each) with sea water of a salinity of the experimental set up and a temperature of -1 °C. All cultures were subjected to a light and dark cycle of 12 hours each. The foraminifers were kept individually in wells of the dishes and their activities (*e.g.* movement, chamber formation) were monitored and recorded daily. The foraminifers could feed *ad libidum* on natural phytoplankton also extracted from ice cores and added to the culture vessels in excess. In the first experiment the culture medium was changed every 3 weeks by transferring the specimens into new wells with fresh algal food. In the second experiment, the specimens were transferred regularly into new wells with algal food each time and different salinities as indicated by bars in Fig. 2 (*e.g.* on experimental day 32 from 52 to 55 psu). The experimental salinities were obtained by adding portions of concentrated seawater (140 psu derived by evaporation of natural seawater at 50 °C) to filtered seawater from the collection site. Salinities were measured with a WTW salinometer and are reported in psu (practical salinity units, which are equivalent to parts per thousand or ‰).

3. Results

In the first experiment (Fig. 1) specimens of *Neogloboquadrina pachyderma* were subjected to a set of different salinities by direct transfer from 34 psu to the respective salinity (group size 6 specimens each). One group was kept as control under 34 psu. Specimens from this group (34 psu) grew regularly by adding chambers to their shells. Thus a representative specimen (for selection of representative specimens see Discussion) grew from an initial size of 150 μm to 320 μm by adding 4 chambers on the

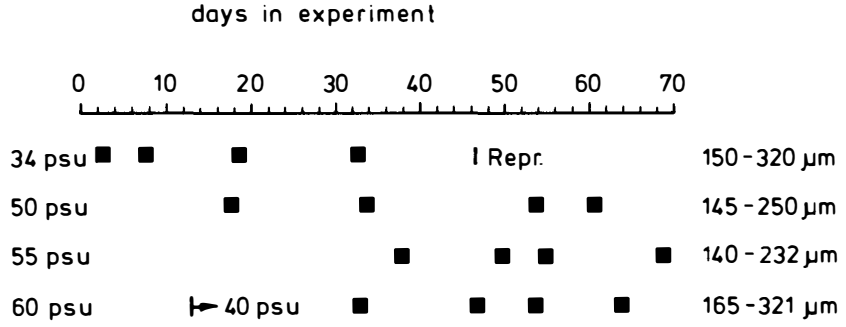

Fig. 1. Chamber formation rates of Neogloboquadrina pachyderma *under different salinity regimes. The black squares indicate the day on which a representative individual formed a new chamber. Also shown are the maximum test diameters at the beginning and the end of the experiment. Note that the specimens originally subjected to 60 psu were transferred back to 40 psu after 13 days of treatment. Repr. =Specimen reproduced by releasing gametes.*

respective days as indicated in Fig. 1. This particular specimen produced gametes on the 47th day in culture; only an empty test remained.

After the transfer to 50 psu the foraminifers remained motionless and did not extend pseudopodia for 2 to 6 days. Chamber formation was also retarded compared to the control group. The first chamber was formed on the 18th day under these conditions and an additional 3 chambers were added in about 60 days by a representative animal. It thus grew from 145 μm to 250 μm, with an overall size smaller than that of the specimen kept under 34 psu.

In specimens subjected to 55 psu no pseudopodia were visible in any of the specimens for 7 days. Thereafter specimens recovered, moved around, and collected diatoms for feeding purposes. Chamber formation again was delayed considerably with the first chamber being built on day 38. After four chambers were added to the test the specimen increased in maximum diameter to 232 μm, being again slightly smaller compared to the specimens from the lower salinity groups.

The specimens which were transferred directly from 34 psu to a salt concentration of 60 psu did not show any signs of life during the first 13 days of the experiment. Pseudopodia were never extended. Thus the foraminifers were not able to move and feed. Since the cytoplasm was gradually diminishing or withdrawn into older parts of the shell, the specimens were regarded as dying or dead. To confirm this, all specimens were transferred back to 40 psu. After 3 to 4 days pseudopodia were visible again and the animals recovered quickly. On day 32 (19 days under 40 psu) the first chamber under experimental conditions was added to the shell. After the formation of 4 chambers a final size comparable to that of the control group was reached.

In a second experiment 6 specimens were serially transferred to increasing salinities

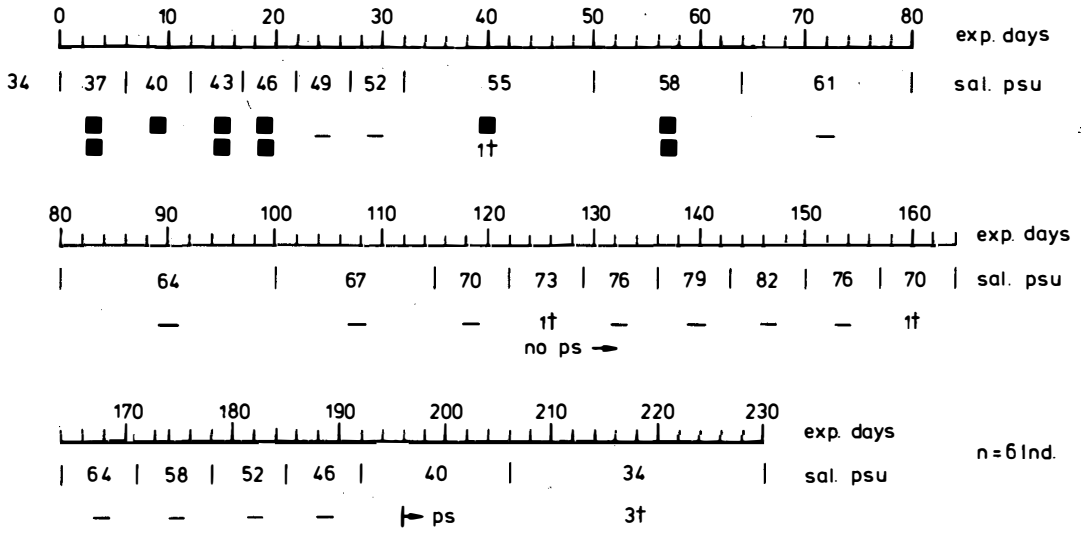

Fig. 2. Salinity experiment with 6 individuals of Neogloboquadrina pachyderma. *During the 230 days of the experiment the specimens were subjected to increasing salinities from 34 psu to a maximum of 82 psu on day 143 in salinity steps of 3 psu. After 7 days under 82 psu salinities were decreased in steps of 6 psu down to 34 psu again. Black squares indicate the number of chambers formed under the respective salinity regime; numbers with crosses indicate dead specimens; no ps and ps indicate that from subjecting the specimens to 73 psu no pseudopodia were observed and were only extended again 4 days after being transferred back to 40 psu.*

up to 82 psu and then to decreasing salinities, and chamber formation was recorded (Fig. 2).

New chambers were added at salinities up to 58 psu, although one individual died at 55 psu after 40 days in culture. In higher salinities no additional chambers were formed and after transfer to 73 psu none of the specimens extended pseudopodia or moved any more, and an additional individual died. The highest salinity, *N. pachyderma* was subjected to was 82 psu for 7 days. Thereafter the salinity was decreased again in steps of 6 psu. A third specimen died after 160 days in culture. The remaining 3 individuals however survived this treatment. After 4 days at a salinity of 40 psu pseudopodia were extended and the foraminifers were able to move and feed again. After being transferred to 34 psu, however, the remaining 3 specimens died between days 220 and 230 (Fig. 2).

4. Discussion

One of the drawbacks of the first experiment of this investigation is that statistical validation was not possible and instead of giving mean data for each group only a representative specimen was chosen. This is partly due to small individual numbers per experimental set-up (6 specimens per group). In addition the life span of specimens from different groups was extremely variable and thus the number of chambers added was also variable. At 34 psu, specimens reached maturity after 30 to 40 days and reproduced. However, at higher salinities reproduction did not occur and some of the specimens lived for more than 200 days while adding smaller chambers than the previous ones (kummerform chambers) to the test. To compare the effects of the salinity on final shell size, specimens had to be chosen which were of roughly the same size at the beginning of the experiment and which had built the same number of chambers.

In the experiments reported here only the effects of salinity were tested. In the natural environment, within the brine channel system of the sea ice, salinities and temperatures are inversely correlated (see Table 1). Low temperatures create high salinities within the sea ice and high salinities are not found within the ice without low temperatures. Thus the experimental set-up does not fully reflect the conditions sympagic organisms are subjected to. However, BARTSCH (1989) tested the combined effects of salinity and temperature on three species of sympagic diatoms (*Amphiprora kufferathii, Nitzschia cylindrus, Thalassiosira antarctica*). She showed that no change in cell division rates occurred in these species tested independently whether they were cultivated in 6 different salinities ranging from 34 to 150 psu either at -1 ℃ or at each of the temperatures corresponding to the elevated salinity. Although results obtained from these diatoms cannot be directly transferred to other organisms, it appears that temperature is not as critical as salinity.

In the natural environment sea ice organisms are released to low salinity water when the sea ice melts and thus have to tolerate salinities lower than that of normal seawater. GRANT and HORNER (1976) demonstrated that the sympagic diatom *Porosira glacialis* grew in salinities from 10 psu and greater and a natural ice microflora increased in cell numbers under a salinity regime of less than 20 psu (VARGO *et al.*, 1986). *Drescheriella glacialis*, a harpacticoid copepod from Antarctic sea ice, tolerated salinities

as low as 20 psu (DAHMS *et al.*, 1990). Therefore one of the intriguing results was found in the second experiment. After exposure to high salinities the foraminifers were transferred back stepwise to normal salinities of 34 psu. At 40 psu the three remaining specimens recovered and recommenced movement. However, after some days at 34 psu these individuals died without further growth and reproduction. A possible explanation may be the overall age of the foraminifers at the end of the experiment. The specimens were obtained from the ice at the beginning of the summer season with the onset of ice melt. From there the specimens were kept for additional 200 days under "winter salinities" before actually being subjected to normal salinity. Thus the specimens attained an age which might not occur in the natural environment and thus were not able to cope these conditions any more. Most other planktonic foraminifers have a lunar cycle and accordingly a life span of about 30 days only (HEMLEBEN *et al.*, 1989).

With these experiments some of the vertical distribution patterns of living and dead foraminifers within ice floes may be explained. SPINDLER and DIECKMANN (1986) have demonstrated that empty shells (dead foraminifers) were mainly found in upper portions of the ice while most living specimens were encountered in lower portions. Since pseudopodial activity ceases at salinities above 73 psu the foraminifers are not able to move and feed in an environment with salinities as high or higher than that. They are able to survive these, and even higher, salinities for some weeks but eventually die of starvation. Low temperatures and high salinities may also be the cause of foraminifers dying in the ice. During winter time temperatures measured in upper parts of ice floes were as low as $-15\,^{\circ}C$ with brine channel salinities of 177 psu (BARTSCH, 1989).

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