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Cold Resistance and Metabolic Responses to Salinity Variations in the Amphipod *Eusirus antarcticus* and the Krill *Euphausia superba*

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Summary. The krill *Euphausia superba*, unlike the amphipod, *Eusirus antarcticus*, tolerates being frozen into solid sea-ice at temperatures down to about −4 °C. Cooled in air, the amphipod and the krill freeze and will die at temperatures of −11° and −9 °C respectively, representing the supercooling points of the animals. The krill is an osmoconformer in the salinity range of 25 to 45 ppt, while the amphipod conforms in the salinity range of 26 to 40 ppt. The animals thereby lower the melting point of their body fluids in the vicinity of the freezing sea ice, preventing internal ice formation at low temperatures. The mean oxygen consumption rates, at raised and lowered salinities, were not significantly different from rates obtained in normal (35 ppt.) seawater, indicating that salinity has little effect on the metabolism of either species.

Introduction

In the Southern Hemisphere polar sea-ice forms a seasonally varying annulus around the Antarctic continent covering up to 10% of the total sea surface at its maximum extent (Zwally et al. 1983). At the ice/water interface of growing ice, salts are included as brine pockets in the ice (Weeks 1968). In response to temperature change and internal stress, the pockets interconnect as brine channels which drain the brine back to the ocean (Untersteiner 1968; Cox and Weeks 1974). The volume and salinity of brine excluded from sea-ice depends on the growth rate of the ice and the salinity of the seawater (Wakatsuchi and Ono 1983).

In the Arctic, melting of the sea-ice surface begins as air temperatures approach freezing point, with a development of melt ponds at the surface of the ice floes (Nansen 1906). Melt ponds are characteristic of melting ice in the Arctic, but have rarely been seen in the Antarctic (Gordon 1981; Maykut 1985) as Antarctic pack ice melts predominantly at the ice/water interface (Andreas and Ackley 1982).

Sea-ice is a habitat for a diverse group of marine animals, but in both the Arctic and the Antarctic the true under-ice fauna is dominated by amphipods (Andriashev 1968; Carey 1985). The dominant species in the ice community of the Barents Sea are *Apherusa glacialis*, *Gammarus wilkitzkii* and *Onisimus glacialis* (Gulliksen 1984; Aarset and Aaunaas 1987a). During the AMERIEZ-86 cruise with USCGC Glacier to the Weddell Sea, the dominant species observed in the ice community were the amphipod *Eusirus antarcticus* and the 1, juvenile stage of the krill *Euphausia superba*.

Microdistribution of amphipods in under-ice habitats varies from species to species (Carey 1985). Individuals have been observed living in brine channels (Cross 1982; Newbury 1983) and partially or fully embedded in the ice (Gulliksen 1984). Green and Steele (1975) reported that *Gammaracanthus loricatus* was the only amphipod species associated with ice stalactites and may at times be frozen within them. In the Weddell Sea, *E. antarcticus* was found living in brine channels or at the ice/water interface. The 1. juvenile stage of the krill *E. superba* was observed on the under surface of the ice feeding on ice algae.

If krill and amphipods are associated with sea-ice throughout the year, they will be exposed to the seasonal changes in physical parameters as the ice melts or freezes. During the summer melt of the ice both species are likely to encounter low salinity conditions, and during sea-ice growth they will be exposed to low temperature and high salinity brine at the ice/water interface. The cold resistance and euryhalinity of *Euphausia superba* and *Eusirus antarcticus* will ultimately determine whether they must leave the sea ice or if they can cope physiologically with the changing conditions. The present study describes cold tolerance and metabolic responses to osmotic stress in the two species in order to better understand the microdistribution of the under-ice fauna in the Antarctic.

Materials and Methods

Animals

The amphipod *Eusirus antarcticus* and the krill *Euphausia superba* were collected in the Weddell Sea, Antarctica at about 63 °S 45 °W in

February–March 1986. The animals were sampled from small pockets in the ice by using a diver operated suction sampler (Aarset and Willumsen 1985). The salinity of the collected seawater was about 34 ppt. and the temperature −1.4° to −1.8 °C.

The animals were transported to the laboratory in thermos bottles and kept in aerated non-filtered seawater at nearly constant temperature (−1° to −1.8 °C) and salinity (34 ppt.) for 24 h. During this period injured animals were removed and recently molted (soft-bodied) individuals were not used further in the experiments. The total length of the amphipods ranged from 20 to 25 mm and the krill from 15 to 25 mm, measured from the base of the antennae to the telson.

Freezing Experiments

Two experiments were performed to assess the behaviour and survival of specimens of *Eusirus antarcticus* and *Euphausia superba* exposed to freezing seawater. Experiments were conducted in a refrigerated bath (Haake) filled with ethanol and water (±0.05 °C). In the first experiment, 3 PVC-bottles (0.5 l) each containing 5 amphipods and 400 ml of seawater (34 ppt., −1.5° to −1.8 °C) were immersed in the refrigerated bath, which was preset to a temperature of −2 °C. The seawater temperature in each bottle, and in the bath, was recorded using thermocouples (28 g copper-constantan) connected to a potentiometric recorder (Leeds and Northrup) as the temperature slowly declined (Aarset and Aunaas 1987b). To mimic ice crystal growth from the sea surface, the seawater was seeded from the top of each bottle.

In three separate runs, the three bottles were cooled to −3°, −4° and −5 °C respectively and allowed to remain at low temperature for 6 h. The bottles were then removed and the ice allowed to melt at room temperature (15°–20 °C). As the seawater approached the melting point (−1.9 °C), it was aerated and the animals observed for mortality. Individuals that were swimming in an apparently normal manner and which displayed normal, cordinated movements were defined as 'surviving". Animals which displayed uncoordinated movements or which did not move at all were defined as "dead". The experiment was repeated with the krill *E. superba.*

In a second experiment, the effects of freezing animals into solid sea ice were studied. Three 20 ml plastic syringes, each containing about 10 ml of seawater (34 ppt., −1.5 °C), a piece of cotton and one animal placed on top of the cotton, were placed in air-filled PVC-bottles in the cooling bath preset to −2 °C (Aarset and Aunaas 1987b). The temperature of the freezing seawater was continously recorded using thermocouples introduced into the water through holes in the plunger. After cooling the system to temperatures of −3°, −4° and −5 °C, the syringes were taken out of the water bath and the seawater samples allowed to thaw slowly at room temperature to examine survivorship, as the seawater approached the melting point (−1.9 °C), according to previously defined criteria.

Supercooling and THF

Supercooling of intact animals blotted dry with filter paper was determined in individual amphipods and krill by cooling them in 20 ml air-filled syringes. Each individual was in continous contact with a thermocouple connected to a temperature recorder. In order to obtain a low rate of cooling, the thermal insulation was increased by wrapping each syringe in cotton and placing it in an air filled PVC-bottle immersed in the cooling bath. The bath was preset to a temperature of −20 °C. This gave a cooling rate of about 0.1 °C/min. The experiment was then repeated with 10 ml of filtered seawater and one animal in each syringe. The presence of thermal hysteresis factors (THF's) in the haemolymph of the animals was determined by measuring temperature differences in haemolymph melting and freezing point (DeVries 1971; Zachariassen and Husby 1982).

Osmotic Experiments

To determine the effect of external salinity on body fluid osmolality of amphipods and krill, the steady state haemolymph osmolality was determined after an acclimation period of 24 h to salinities ranging from 25 to 45 ppt, at a temperature of 0° to 1 °C. Samples of haemolymph were taken from 3 to 4 individuals at each exposure salinity. Concentrated seawater was prepared by adding hypersaline water made by freezing.

Respiratory Measurements

Oxygen consumption rates were determined by allowing individuals to deplete the oxygen in a sealed water-jacketed chamber filled with seawater at the desired experimental salinity. Respiratory determinations were made at 26, 35 and 40 ppt for *Eusirus antarcticus* and at 25, 35, 45 ppt for *Euphausia superba.* Individuals were acclimated to salinity for a period of 24 h. Temperature was maintained at 0.5 °C (±0.1 °C) using a circulating refrigerated water bath. Oxygen partial pressure was continously monitoried using a Clark polarographic oxygen electrode (Clark 1956) as the individual reduced oxygen levels to intermediate (40 to 60 mm Hg) partial pressures. Electrodes were calibrated using air- and nitrogen-saturated seawater at the experimental temperature (Childress 1971). The time required for consumption of oxygen to intermediate levels varied from 4 to 8 h.

Chambers were constructed entirely of lucite in rectangular configuration. A perforated lucite false bottom isolated experimental subjects from a stirring bar that was used to insure homogeneity within each chamber. The lowest possible stirring speed was used to minimize disturbance. All experiments took place in the dark with brief periods of observation in low light.

Data were recorded using a computer-controlled digital data-logging system. Each oxygen probe was scanned once per minute, its signal being averaged over a period of 1 s, and then recorded. Data were reduced by first averaging the 30 recorded values in each 30 min increment of an entire 4 to 8 h experiment, producing between 8 and 16 30-min points per run. The first hour was discarded due to the very high activity associated with introduction into the respirometer. All 30-min points thereafter, down to an oxygen partial pressure (PO_2) of 80 mm Hg, were averaged to produce a routine rate for each individual. Maximum rates were the maximum 30-min rate and minimum rates the minimum 30-min rate recorded for each individual after the first hour for values above a PO_2 of 80 mm Hg. Most often, maximum rates were associated with the beginning of the experiments. Minimum rates generally occurred during intermediate portions of a run.

After the termination of each respiratory run, specimens were blotted dry, placed in a polypropylene vial, and frozen. In the laboratory, specimens were thawed and weighed wet, then dried in a 60 °C oven to constant weight, and reweighed to determine dry weight.

Sampling and Analytical Methods

Samples of haemolymph were obtained by inserting a pointed, paraffin-filled glass capillary dorsally through the inter-segmental membrane. After taking a sample (5–20 µl) the capillary was sealed at one end by melting, and centrifuged in a Compur 1100 microcentrifuge, leaving the haemolymph sample isolated under a layer of paraffin oil (Zachariassen et al. 1982). Capillaries were stored in a deep freeze (−20 °C) prior to analysis. Seawater salinity was measured on an Atago refractometer. The osmolality of the haemolymph was determined by a Clifton nanolitre osmometer and Wescor standards, from the melting point of samples with a volume of 30–50 nl.

Results

Freezing Experiments

In the first experiment, ice crystals grew from the sea surface downward in each bottle, until both the ice and the unfrozen seawater fraction reached ambient temperatures of −3°, −4° and −5 °C, representing the melting point of

the brine at the ice/water interface in each case (Maykut 1985). During the experiment, the majority of the amphipods stayed in the unfrozen seawater fraction, with only very few freezing into the ice. In contrast, the krill aggregated at the sea ice and frequently froze into the ice.

The median lethal temperatures (the temperature at which 50% of the individuals die) of *E. antarcticus* and *E. superba* following cooling in freezing seawater is presented in Table 1. None of the animals were injured when cooled to −2 °C, however, all the amphipods died after an exposure to −3 °C. Krill were relatively unharmed at this temperature. Assuming that this is the melting point of the unfrozen seawater fraction, this point corresponds to a salinity of 52 ppt. All the krill died at a temperature of −5 °C, or a brine salinity of 85 ppt. In the temperature range of −3° to −5 °C, per cent mortality increased rapidly with about 60% survival at −4 °C or a brine salinity of 69 ppt. In the second experiment, the effect of freezing animals into solid sea ice was studied (Table 2). All amphipods died when frozen solid into sea ice. The krill, however, tolerated being frozen into the ice at a median lethal temperature of about −4.1 °C.

Table 1. Low temperature exposure (Median Lethal Temperature) of *Eusirus antarcticus* and *Euphausia superba* in PVC-bottles containing seawater/ice

Species	Number of samples	Exposure temp. °C	Time (h)	Median LT °C (mean ± SD)
E. superba	60	−2 to −5	6	−4.2 ± 0.4
E. antarcticus	45	−2 to −4	6	−2.5 ± 0.2

Table 2. Low temperature exposure (Median Lethal Temperature) of the amphipod *Eusirus antarcticus* and the krill *Euphausia superba* in solid sea ice and in supercooled 34 ppt. seawater

Species	Number of samples	Frozen solid Median LT °C	Supercooled Median LT °C
E. superba	12	−4.1	
	8		−6 to −7
E. antarcticus	12	−2.4	
	7		−3 to −4

Supercooling and THF

The mean and standard deviation of the supercooling point in air of 6 krill was −9.0 ± 1.6 °C and 3 amphipods −11.4° ± 0.6 °C (Table 3). Supercooling points were indicated by a sudden increase in temperature due to the release of heat of crystallisation (fusion) of water. Supercooling of animals in filtered seawater was interrupted by spontanious ice crystallization. However, the krill were able to survive to at least −6 °C and the amphipod to at least −3 °C (Table 2). There was no significant difference (Student's-*t*-test) between the melting and freezing point of the haemolymph of either the krill (d.f. = 6, $P > 0.05$) or the amphipod (d.f. = 4, $P > 0.05$) indicating that no thermal hysteresis was present (Table 3).

Osmotic Experiments

The haemolymph steady state osmotic strength in amphipods and krill, at a temperature of −1.5° to 0 °C, was determined after an acclimation period of 24 h to different experimental media. The amphipod *E. antarcticus* was an osmoconformer in the salinity range 26 to 40 ppt. (Fig. 1). The regression line for haemolymph (y) vs salinity (x) was calculated for 11 pairs of observations by the method of least squares. The slope (34.3) of the regression line did not differ significantly (Student's-*t*-test, d.f. = 10, $P > 0.05$) from the point estimate of the slope (33.3) of the isosmotic line. The confidence interval for the difference between the two slopes was 1.00 ± 2.245. The intercept (−136.2) of the regression line did not differ significantly (Student's-*t*-test, d.f. = 11, $P < 0.05$) from the point estimate of the intercept (−133) of the isosmotic line.

The krill *E. superba* was an osmoconformer in the salinity range of 25 to 45 ppt. (Fig. 2). The regression line for haemolymph (y) vs salinity (x) was calculated for 12 pair of observations by the method of least squares. The slope (32.6) of the regression line did not differ significantly (Student's-*t*-test d.f. = 11, $P > 0.05$) from the point estimate of the slope (33.3) of the isosmotic line. The confidence interval for the difference between the two slopes was 0.70 ± 1.99. The intercept of the regression line (−83.9) did not differ significantly (Student's-*t*-test d.f. = 12, $P > 0.05$) from the point estimate of the intercept (−133) of the isosmotic line.

Table 3. Thermal data (°C) of the amphipod *Eusirus antarcticus* and the krill *Euphausia superba*. Δ_{scp} = supercooling point, Δ_f = freezing point, Δ_m = melting point ($\bar{X} \pm SD$)

Species	Number of samples	Δ_{scp}	Δ_f	Δ_m	$\Delta_f - \Delta_m$
Eusirus antarcticus	3_a	−11.4 ± 0.6			
	3_b		−1.98 ± 0.06	−1.95 ± 0.07	−0.03 ± 0.09
Euphausia superb	6_a	−9.0 ± 1.6			
	4_b		−2.00 ± 0.09	−1.96 ± 0.08	−0.04 ± 0.12
	3_c			−1.91 ± 0.05	

a = intact animals, b = haemolymph, c = medium seawater

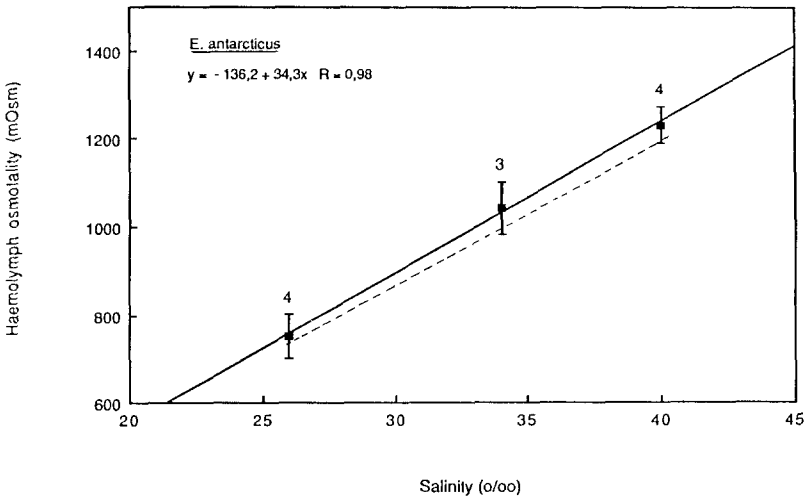

Fig. 1. Haemolymph osmolality (mmole/kg H_2O as mOsm) of *Eusirus antarcticus* acclimated for 24 h to various seawater salinities. The data are given as mean ± SD with number of individuals indicated above each bar. The *solid line* represents the regression line of the haemolymph osmolality (y) vs salinity (x). The *dotted line* shows an isosmotic condition

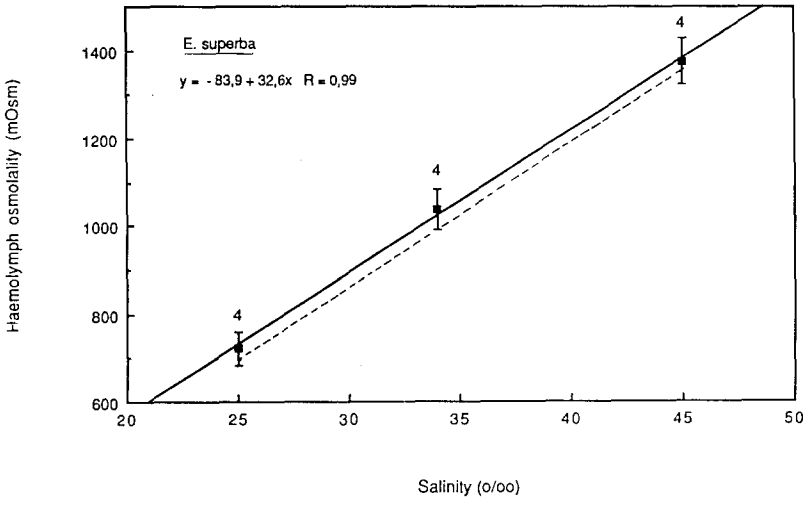

Fig. 2. Haemolymph osmolality (mmole/kg H_2O as mOsm) of *Euphausia superba* acclimated for 24 h to various seawater salinities. The data are given as Mean ± SD with number of individuals indicated above each bar. The *solid line* represents the regression line of the haemolymph osmolality (y) vs salinity (x). The *dotted line* represents an isosmotic condition

Respiratory Measurements

Eusirus antarcticus and *Euphausia superba* showed slightly elevated mean oxygen consumption rates at the raised (40 ppt. or 45 ppt.) and lowered (26 ppt., 25 ppt.) salinity, compared with rates in normal (35 ppt.) seawater (Figs. 3 and 4). However, the differences in rates were not significant (Anova: amphipod, $F(2, 29) = 3.2$, $P > 0.05$, krill, $F(2, 21 = 2.9$ $P > 0.05$).

Discussion

The present study indicates that the krill *Euphausia superba* unlike the amphipod, *Eusirus antarcticus* tolerates being frozen into solid sea ice at temperatures down to about −4 °C (Tables 1 and 2). Although both are mobile species, the amphipods avoided the growing ice front during freezing experiments while the krill did not. The results correlate well with underwater observations made in the Weddell Sea. During several dives underneath the polar pack ice, underwater frazil ice formation was observed. Ice core data have indicated that the congelation ice in the Weddell Sea accounts for about 20% of the multiyear ice and 47% of first year ice, with fine grain layers of frazil crystals making up most of the remainder (Maykut 1985). The frazil ice accumulated on the undersurface of the ice making up a 20 − 30 cm thick ice crystal layer. Amphipods left the congelation ice during freeze-up, crawled through the frazil ice layer and took up a position at the interface of the frazil ice crystal and surrounding seawater. *E. superba* largely disappeared during freezing episodes, but it was difficult to observe any individuals frozen into the ice.

When individuals of *E. antarcticus* and *E. superba* were cooled in air, they froze and died at temperatures of −11.4° ± 0.6 °C and −9.0° ± 1.6 °C respectively (Table 3). The relatively low supercooling points indicate that no potent nucleators were present in the body fluids of the animals (Zachariassen 1980). The amphipod *Gammarus wilkitzkii* from the Arctic was found to supercool to about −4 °C using identical techniques to those in the present study. Similarly, the amphipod *Gammarus oceanicus* associated with landfast ice at Spitsbergen has a supercooling

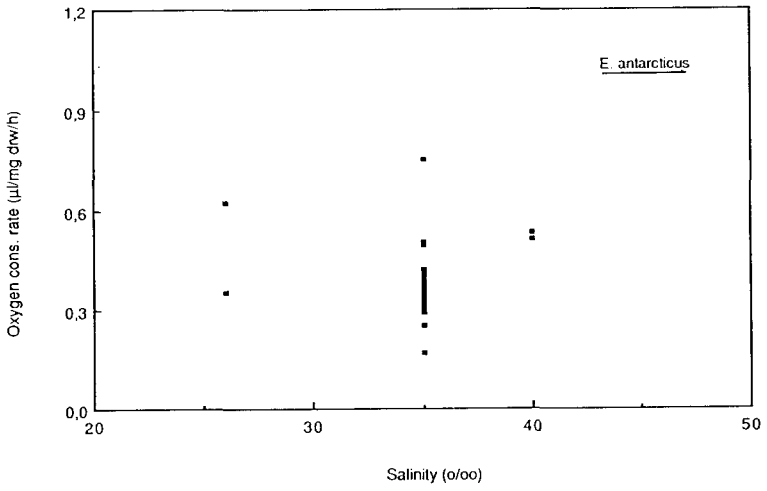

Fig. 3. Oxygen consumption rates (μl O_2 mg dry weight^{-1} h^{-1}) of *Eusirus antarcticus* acclimated for 24 h to various seawater salinities. Each point represents one amphipod

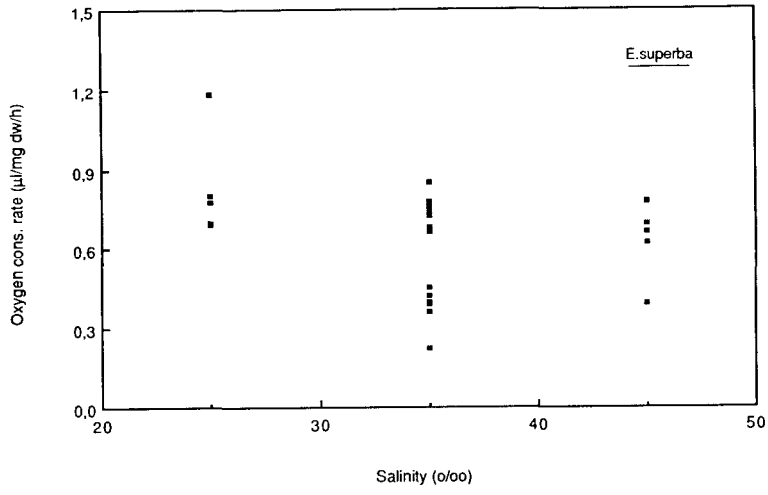

Fig. 4. Oxygen consumption rates (μl O_2 mg dry weight^{-1} h^{-1}) of *Euphausia superba* acclimated for 24 h to various seawater salinities. Each point represents one animal

point of about −6.0 °C (Aarset and Aunaas 1987b). The Antarctic under-ice fauna appear to have a better supercooling capacity than the Arctic species so far investigated.

Rakusa-Suszczewski and McWhinnie (1976) studied the super-cooling capacity of benthic and pelagic Antarctic fauna supercooled in filtered seawater. The supercooling capacity was in the range of −4° to −8 °C and ice formation started on gill surfaces and appendages of the animals. Our experiments with individuals supercooled in filtered seawater yielded similar results (range −3° to −6 °C, Table 2). However, it was difficult to decide where the ice nucleation initiated, as an internal nucleation in the body fluids of the animals, or as a nucleation in the seawater initiated mechanically by the legs and spines of the animals. As individuals can be supercooled to a lower temperature in air, representing internal ice nucleation, it is probable that ice nucleation initiated in filtered seawater at a higher temperature is of external origin.

Survival of *E. antarcticus* and *E. superba* in a supercooled state could depend on thermal hysteresis agents present in their body fluids. These are proteinaceous compounds acting to stabilize the supercooled state and have been demonstrated in different catogaries of supercooled animals (DeVries 1971; Zachariassen and Husby 1982). However, tests for thermal hysteresis agents were all negative (Table 3). The fact that animals cooled in freezing seawater were injured at temperatures above those of animals cooled in air suggests that mechanisms additional to spontaneous internal freezing were causing injury.

In the freezing experiments, some individuals of both species left the ice during freezing but tolerated the increasingly concentrated brine. Low temperatures seem to promote the salt tolerance of both the krill and the amphipods. These results correspond well with observations of other crustaceans (Kinne 1964; Dorgelo 1977; Aarset and Aunaas 1987b).

When animals were exposed to high salinity media at constant temperature, they conformed osmotically within the tolerated salinity range (Figs. 1 and 2). The results are similar to those found in studies of the amphipod *Orchomene plebs* in Antarctic sub-ice communities (Rakusa-Suszczewski and McWhinnie 1976) and the krill *Meganyctiphanes norvegica* from Norwegian waters (Forward and Fyhn 1983). During sea ice growth, both species are

able to stay in the vicinity of the ice, conforming to the ambient brine salinity. The animals thereby lower the melting point of their body fluid. The conclusion assumes that the cooling rate of the medium is slow enough to allow a gradual increase in the salinity of the brine sufficient for an osmolality adjustment in the haemolymph of the animals. Similar results have been reported for the under-ice amphipod *Gammarus wilkitzkii* from the Arctic (Aarset and Aunaas 1987b).

During summer, most of the Antarctic pack ice melts at the ice/water interface with a relatively low input of freshwater to the sea surface (Gordon 1981; Maykut 1985). Exposure of *Eusirus antarcticus* and *Euphausia superba* to low salinity media at a temperature of about 0° to −1 °C demonstrated that the animals were osmoconformers over their tolerated salinity range (Figs. 1 and 2). The Antarctic species were not as euryhaline as the under-ice amphipods from the Arctic, which have the ability to hyperosmotically regulate down almost to freshwater (Aarset and Aunaas 1987a). This might be a response to differences in the melt progression of the two polar regions with the most significant input of meltwater to the sea surface in the Arctic.

Salinity had little effect on the mean oxygen consumption rates of *Eusirus antarcticus* and *Euphausia superba* in the tolerated salinity ranges (Figs. 3 and 4). The rates at low and high salinities fall easily within the range recorded at normal oceanic salinity (Table 4) (35 ppt.) and as such are not significantly different. However, the slightly elevated mean oxygen consumption rates were at the upper end of the range of variability observed during the course of individual respiratory determinations, and between individuals. Normally, differences in spontaneous locomotory activity produce occasional values as low as 40% and as high as 200% of the overall mean during the course of an individual run. As the values at low and high salinity in both species are elevated above the mean at 35 ppt it suggests an extra energy expenditure associated with residing at salinity higher or lower than 35 ppt. It is unclear whether the extra metabolic work is due to a locomotory response (escape), to stress, or to work associated with cell and tissue response to osmotic change.

Results of the present study largly agree with those presented by Rakusa-Suszczewski and McWhinnie (1976) for the ubiquitous Antarctic amphipod *Orchomenella plebs*. In the case of *O. plebs* exposure to salinities of 27 ppt. and 43 ppt. resulted in metabolic rates elevated above those recorded at 35 ppt. after a period of 6 h. The rate at 43 ppt. was significantly different from that at 35 ppt. but the rate at 27 ppt. was not. Osmotic change in the osmoconformer *O. plebs* was essentially complete within 6 h. Both *Euphausia superba* and *Eusirus antarcticus* had also reached steady state osmolality in the 24 h acclimation period prior to metabolic rate determinations by end-point blood osmolality. The observed independence from salinity in the metabolism of the krill and amphipod is energetically favourable in the changing salinities of the under-ice habitat.

Table 4. Range of metabolic rates at 35 ppt. Values are expressed as $\bar{X} \pm SD$

Species	*n*	Oxygen consumption rate $\mu l\ O_2$ mg dry $wt^{-1}\ h^{-1}$		
		Minimum	Routine	Maximum
Euphausia superba	14	0.351±0.216	0.605±0.184	1.083±0.480
Eusirus antarcticus	26	0.141±0.202	0.352±0.071	0.732±0.181

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