Ecophysiological studies on arthropods from Spitsbergen

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The cold-hardiness, high temperature tolerance and metabolic activity of summer specimens of staphylinid beetles (*Atheta graminicola*), collembolans (*Onichiurus groenlandicus*), spiders (*Erigone arctica*), and prostigmatid mites (*Molgus littoralis*) from Spitsbergen were investigated. The animals displayed cold-hardiness and haemolymph melting points within the normal ranges for summer insects from temperate regions, but were less tolerant to high temperatures. Haemolymph from spiders and from one species of collembolans (*Isotoma* sp.) was found to contain thermal hysteresis factors. The beetles, collembolans, and mites were found to have oxygen consumption rates above the values of their relatives in other climatic zones, whereas the spiders had values within the range of temperate arachnoids. The study supports the view that polar arthropods have activation energy values lower than those of temperate animals.

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Introduction

Several studies have revealed that mammals and birds from Spitsbergen are physiologically highly specialized (Krog et al. 1976; Grammeltvedt & Steen 1978; Ringberg & Reimers 1982). These specializations apparently reflect adaptations to the prevailing climatic conditions on the islands.

Although the invertebrate fauna at Spitsbergen is fairly well known (Sømme 1979), very few studies have been made on the possible physiological adaptations of the Spitsbergen arthropods. The purpose of the present study was to investigate the cold-hardiness and possible metabolic adaptations of the terrestrial arthropods in this area.

Materials and methods

The investigations were carried out on insects and arachnoids collected in the vicinity of Longyearbyen in mid June 1981 and in the vicinity of Ny-Ålesund at the end of July 1982. The animals were collected under stones on the tundra or in the rich vegetation below bird cliffs in Kongsfjorden. The animals were kept in small glass tubes at temperatures ranging from +2 to −2°C for up to ten days before they were used in the experiments. The experiments were carried out partly in a temporary laboratory established in a cabin in Adventdalen and partly at the research station of the Norwegian Polar Research Institute in Ny-Ålesund.

The supercooling points of the animals were determined by using the arrangement shown in Fig. 1a. The animals were attached to a DM thermistor probe of a Grant temperature recorder by means of silicone grease. They were cooled inside a thermos bottle containing a cold mixture made from snow and $CaCl_2 \cdot 6H_2O$. The supercooling points were indicated as small inflections on the temperature curve, due to the release of the heat of fusion of water freezing.

The melting points of the haemolymph of the animals were determined by using a Clifton nanolitre osmometer, in which the melting process of 30 nl samples of haemolymph could be observed in a microscope, while the temperature of the samples was regulated with an accuracy of ± 0.001°C. The temperature at which the last tiny ice crystal disappeared during slow warming of the sample was taken as the melting point. Samples of haemolymph were obtained from the animals by puncturing the cuticle with a thin glass capillary and sucking the haemolymph into the capillary by means of the capillary forces. When a sufficient amount of haemolymph could not be obtained from one animal, the samples were pooled from several individuals. The haemolymph samples were handled as described by Zachariassen et al. (1982).

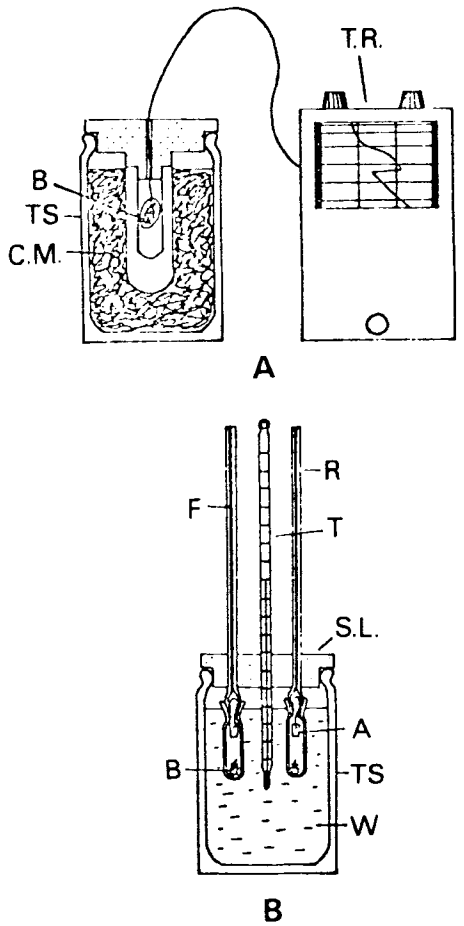

Fig. 1. A: Arrangement of instruments for determination of supercooling points. B—animal. C.M.—cold mixture. TS—thermos. T.R.—Grant temperature recorder. B: Arrangement of instruments for determination of oxygen consumption. B—animal. A—CO_2 absorber (10% solution of KOH). R—respirometer. S.L.—styrofoam lid. T—thermometer. TS—thermos. W—water. F—indicator fluid.

The presence in the haemolymph of thermal hysteresis factors (THF), which have the ability to separate the temperature of ice crystal growth upon cooling of a frozen sample from the melting point, was investigated on the Clifton nanolitre osmometer as described by Zachariassen & Husby (1982a). The haemolymph samples were cooled with a tiny ice crystal present, and the temperature at which a rapid growth of the ice crystals was observed was taken as the hysteresis freezing point (HFP).

The upper lethal temperatures of the animals were determined by exposing them to temperatures increased in steps of 5°C until they showed abnormal behaviour (uncoordinated walking) or died. The animals were exposed to each temperature for 10 min. The experiments were performed with the animals kept within small glass tubes which were immersed in water baths of the desired temperature.

The oxygen consumption of the animals was measured at different temperatures by using Engelmann constant pressure respirometers, the inner capillary diameter of which is 0.5 mm (Engelmann 1963). In order to obtain constant temperatures, the respirometers were immersed in waterfilled thermos bottles as shown in Fig. 1b. Up to five animals were used in each respirometer. A piece of paper was put into the respirometers to give the animals a convenient substratum and thus keep their activity at a low level. In order to adjust for possible variations in temperature or atmospheric barometric pressure, an empty respirometer was used as a blank instrument. The oxygen consumption was calculated at NTP and in relation to the fresh body weight of the animals.

Since no balance was available in the field laboratories, the fresh body weight had to be determined by means of an indirect method after return to the University. Some of the animals, particularly the collembolans, became seriously dehydrated during the respirometer experiments, and the fresh body weight was estimated from the dry weight. Immediately after the experiments the animals were transferred to dry, clean glass tubes, in which they were dried to a constant weight at +60°C. The relative water content of each species was determined on specimens that were transported alive to the University of Trondheim, and these data were used to estimate the fresh body weights of the experimental animals from the dry weight values. The relative water content of the animals varied from about 75% for the collembolans and mites to about 61% for the beetles. The oxygen consumption was calculated in relation to the estimated initial fresh body weights.

Results

The melting points, hysteresis freezing points, supercooling points, and upper lethal temperatures of the animals are shown in Table 1. The data reveal that all species investigated had haemolymph melting points in the range of from

Table 1. Melting points, hysteresis freezing points, supercooling points and upper lethal temperatures of Spitsbergen arthropods. Values are Mean ± SD, and the number of measurements are given in parentheses.

Species	Melting point (°C)	Hysteresis freezing point (°C)	Supercooling point (°C)	Upper lethal temperature (°C)
Erigone arctica	−1.06	−1.31	−6.4 ± 0.6 (6)	+35 – +40
Molgus littoralis	−1.02	−1.02	−6.0 ± 1.1 (7)	—
Onichiurus groenlandicus	−0.31	−0.31	−6.7 ± 1.7 (11)	+30 – +35
Isotoma sp.	−0.75	−0.90	—	—
Hypogastrura sp.	—	—	−7.1 ± 1.7 (10)	—
Atheta graminicola	−1.03	−1.03	−5.3 ± 1.1 (7)	+30 – +35

Table 2. Oxygen comsumption (mm^3 O_2/g·min) of Spitsbergen arthropods at different temperatures. Values are mean ± SE. The numbers of measurements are given in parentheses.

Species	Temperature (°C) 0	+5	+10	+15
Erigone arctica	1.1 ± 0.4 (2)	2.1 ± 0.3 (7)	1.7 ± 0.5 (4)	3.4 ± 1.2 (4)
Molgus littoralis	1.4 ± 0.3 (3)	5.0 ± 1.5 (3)	6.7 ± 1.0 (3)	14.0 ± 1.4 (3)
Onichiurus groenlandicus	5.9 ± 0.8 (5)	9.9 ± 2.4 (6)	14.0 ± 5.8 (5)	—
Atheta graminicola	5.4 ± 1.3 (3)	10.6 ± 1.1 (4)	13.7 ± 1.8 (4)	26.8 ± 1.3 (4)

about −1.2 to about −0.3°C. In most of the species the freezing point corresponds to the melting point, indicating that THF are absent from their haemolymph. However, the haemolymph of the spiders and one species of collembolans (*Isotoma* sp.) showed a moderate hysteresis, revealing the presence of THF in the haemolymph of these species.

All species had supercooling points within the range of from −5 to −7°C. None of the animals were tolerant to freezing, and thus, the supercooling points correspond to the lower lethal temperatures of the animals. The upper lethal temperatures range from +30 to +35°C for the collembolans and the beetles, and from +35 to +40°C for the spiders.

The oxygen consumption values of each species at different temperatures are listed in Table 2. The results show that the mites, collembolans, and beetles have an oxygen consumption considerably higher than that of spiders.

In order to study the temperature dependence of the metabolic processes more exactly, the data are plotted in an Arrhenius plot (Fig. 2). The Arrhenius plot is based on the Arrhenius equation $M = a \cdot e^{-\mu/R \cdot T}$, where M is the metabolic rate (= oxygen consumption), a is a constant, μ is the activation energy, R is the universal gas constant, and T is the temperature in °K. The Arrhenius equation can be expressed as $ln\, M = ln\, a - (\mu/R)\,(1/T)$, where $ln\, M$ and $1/T$ are used directly in the plot by being linearly related variables. The terms $ln\, a$ and $-\mu/R$ represent the ordinate interception point and the slope, respectively, and can be determined by calculating the linear regression line of the values of $ln\, M$ and $1/T$.

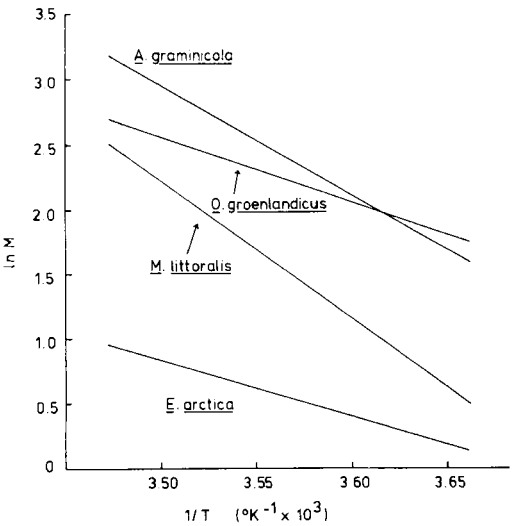

Fig. 2. Arrhenius plot of the metabolic rates of four species of terrestrial arthropods from Spitsbergen. The lines are linear regression lines, calculated as described in the text.

Table 3. Q_{10} values and activation energy values of Spitsbergen arthropods. The correlation coefficient (r) and the number of observations for each species (n) are also given.

Species	Q_{10}	Activation energy (kcal/mol)	r	n
Erigone arctica	1.9	6.9	−0.41	17
Molgus littoralis	3.4	21.1	−0.91	12
Onichiurus groenlandicus	2.3	9.8	−0.41	16
Atheta graminicola	2.8	16.6	−0.92	15

The activation energy is calculated by multiplying the slope of the regression line by the universal gas constant (1.98 cal/mol·°K). The values for the activation energy of the Spitsbergen arthropods are given in Table 3, together with the Q_{10} values of the oxygen consumption. The data show that the activation energy varies from about 7 kcal/mol for the spider to about 21 kcal/mol for the mite. The Q_{10} values vary from 1.9 for the spider to 3.4 for the mite. The values for the insect are between these extremes.

Discussion

The observed melting points of the haemolymph of the Spitsbergen arthropods (−1.2 to −0.3°C) are typical for insects and spiders lacking accumulated polyols in their body fluid (Zachariassen 1980). This conforms well with the observed supercooling points (−5 to −7°C), which are in the range characteristic of temperate summer adapted insects (Sømme & Conradi-Larsen 1977; Zachariassen 1980). Thus, the summer insects at Spitsbergen seem to be similar to summer insects in temperate and tropical regions.

This pattern appears to be disturbed by the presence of thermal hysteresis factors (THF) in the haemolymph of the spiders and in one species of collembolans. The latter observation may suggest that several species of the Spitsbergen arthropods are able to survive prolonged exposures at moderately low subzero temperatures in the summer, even when in direct contact with external ice (Zachariassen & Husby 1982b).

Studies by Duman (1977, 1979) have revealed that the levels of THF vary considerably over the year, from moderate levels or absence during the summer, to a hysteresis range of up to about 6°C in the winter. Since the Spitsbergen arthropods are likely to spend an extremely long period in a hibernating state, those which are sensitive to freezing probably depend heavily on THF to stabilize the unfrozen state and thus avoid a lethal freezing. Consequently, the THF levels of hibernating Spitsbergen arthropods are likely to be considerably higher than those observed in the summer specimens. Furthermore, high levels of THF may well be present during the winter in species lacking such substances in the summer.

Block & Young (1978) found that Antarctic cryptostigmate and mesostigmate mites had oxygen consumption rates higher than those of temperate species, whereas the oxygen consumption of prostigmate mites was lower than the values of temperate mites. Block (1981) obtained results indicating that sub-Antarctic beetles have oxygen consumption rates somewhat below the values found in alpine temperate species (Hågvar & Østbye 1974), but that sub-Arctic collembolans had rates which were somewhat higher than those of collembolans from temperate alpine regions (Conradi-Larsen 1974). In order to compare the oxygen consumption of the Spitsbergen arthropods with the values of arthropods from other

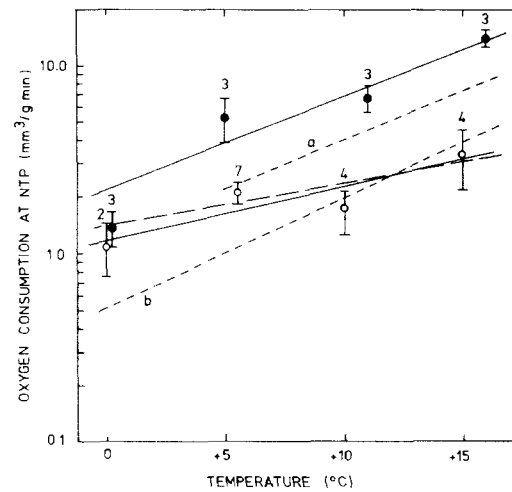

Fig. 3. Semilogarithmic plot of the oxygen consumption of arachnids from Spitsbergen and other regions as a function of temperature. ——: Spitsbergen spiders *Erigone arctica* (○) and mites *Molgus littoralis* (●); – – –: Temperate zone spiders from Finse (line a) (Hågvar & Østbye 1974; Steigen 1976) and temperate cryptostigmatid mites (line b) (Young 1979); — —: Antarctic mite (Young 1979). The lines are linear regression lines. The lines representing values for Spitsbergen animals are calculated from the individual values forming the basis for the data in Table 2, whereas the other lines are calculated from the mean values tabulated in the articles referred to. The bars represent SE and the number of parallel measurements are indicated on the top of each bar.

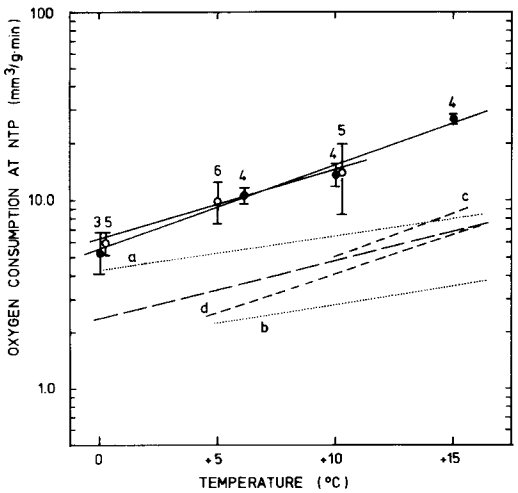

Fig. 4. Semilogarithmic plot of the oxygen consumption of insects from Spitsbergen and other regions as a function of temperature. ——: Spitsbergen collembolans *Onichiurus groenlandicus* (○) and staphylinid beetles *Atheta graminicola* (●); ·····: Sub-Antarctic collembolans (line a) (Block 1981) and beetles (line b) (Block 1981); – – –: Alpine temperate zone beetles (line c) (five species from Finse studied by Hågvar & Østbye 1974) and alpine temperate zone collembolans (line d) (two species from Finse studied by Conradi-Larsen 1974); — —: two species of curculionid beetles from Mount Kenya (Zachariassen, unpublished). The bars represent SE and the number of parallel measurements are indicated on the top of each bar.

regions, the values have been plotted together in Figs. 3 and 4.

Figure 3 shows that *Erigone* spiders from Spitsbergen have oxygen uptake rates which are lower than the values of temperate alpine spiders from the Finse high mountain plateau in Norway over most of the temperature range, but which agree fairly well with the temperature range where the Spitsbergen spiders perform their activity in nature, i.e. 0 – +5°C (personal observations). Mites from Spitsbergen, on the other hand, have oxygen consumption rates considerably higher than those of temperate mites: these results conform with those obtained by Young (1979).

Figure 4 shows that the Spitsbergen collembolans and beetles have oxygen consumption rates considerably above the values of insects from other regions. It is tempting to interpret these results to mean that the Spitsbergen insects are active at relatively low temperatures, and that they have to increase their metabolic rate in order to complete their development within the relatively short summer period. The somewhat deviating results obtained for the spiders may mean that these animals survive in the area due to other strategies, such as reduced development rate and ability to complete their development over several years.

It has also been speculated whether a low oxygen consumption rate may cause more energy to be invested in growth, and thus that animals with a low oxygen consumption rate in fact grow and develop faster than animals oxidizing their food at a high rate (Block & Young 1978). However, it should be kept in mind that protein synthesis and growth also require energy, and that a high growth rate is likely to be accompanied by a high rate of oxygen consumption. Considerably more data are needed on the biological features of the animals and the climatic conditions under which they live, before firm conclusions regarding the physiological adaptations of the terrestrial invertebrates can be drawn.

Young (1979) and Block & Young (1978) calculated the activation energy of different Antarctic and sub-Antarctic arthropods, and found that the values were generally within the lower part of the range of values found for temperate animals. These authors concluded that the activation energy values seem to vary systematically with the prevailing temperature in the habitat of the animals. Figure 5 shows the values of activation energy of Spitsbergen arthropods, plotted in frequency distribution histogram, together with values of temperate, alpine temperate, sub-Antarctic, and Antarctic arthropods. The Spitsbergen animals seem to have activation energy values in the lower range, quite similar to the Antarctic arthropods studied by Block and Young. Moreover, measurements carried out on tropical desert insects have shown that these insects have

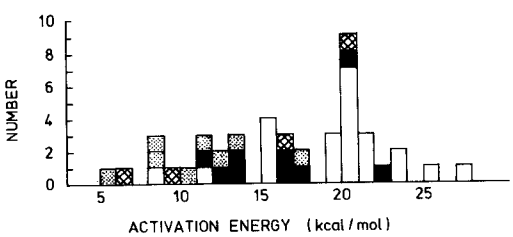

Fig. 5. Frequency distribution of activation energy of polar and temperate arthropods. □: Temperate mites (Young 1979); ■: Alpine temperate arthropods (Conradi-Larsen 1974; Hågvar & Østbye 1974; Steigen 1976); ▨ Antarctic and sub-Antarctic arthropods (Young 1979; Block 1981); ▩ Spitsbergen arthropods (Table 3 in present study).

extremely high activation energy values (Zachariassen pers. comm.). These observations provide further support to the view that the activation energy reflects the predominant temperature conditions under which a species lives.

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