

Thermal resistance and behaviour of the isopod *Saduria entomon* (L.)

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Saduria entomon (Crustacea: Isopoda) occurs as a stenothermal glacial relict in the Baltic. The temperature for the loss of the righting reflex (= critical thermal maximum, CTMax) of the animals collected in winter and kept at 4°C was about 26°C and that for the cessation of pleopod beating about 31°C. When the animals were kept for 1 to 2 weeks at 14°C (warm acclimation), the CTMax did not change but the temperature for the cessation of pleopod beating increased about 1–2 degrees compared to the values for animals kept at 4°C. The onset of locomotory inactivity was observed at around 15°C with continuously increasing temperature; this temperature was not changed by warm acclimation of the animals. *Saduria* collected at the end of the summer (warm acclimatization) exhibited adaptive changes in all of the motor functions mentioned above. When measured at 4 and 14°C, the rate of the pleopod beating of *Saduria* kept previously at 4 and 14°C exhibited an inverse acclimation at 14°C. In order to test the thermal orientation behaviour of *Saduria*, a toroidal temperature gradient apparatus with gradients of 2–17°C and 9–24°C was used. The animals kept previously at 4°C selected a temperature of about 15°C and came to rest at this temperature in both of the gradients.

1. Introduction

Saduria entomon (L.) is an arctic marine-estuarine isopod crustacean, which occurs as a glacial relict in the Baltic Sea. In the Baltic, it typically lives at depths of 10–30 m and below, and so is seldom exposed to large variations of light intensity and temperature. The temperature at a depth of 40 m in the northern Baltic varies between 0.5 and 10°C. At 30 m it lies below 5°C for at least 10 months of the year. *Saduria* is a stenothermic cold water animal. The aim of the present study was to

determine the effect of temperature on the motor activity of *Saduria*.

2. Materials and methods

Saduria entomon were collected in February at Rymättylä (Turku archipelago). The animals were kept in the laboratory in Baltic sea water (salinity 6‰) at 4°C for from 1 week to 4 months. A group of the animals was kept at 14°C for 1 to 2 weeks. Some animals were collected in September at

Seili (Turku archipelago) and kept at 13°C for 1 to 2 weeks. The animals were fed with fish meat and the water in the tanks was changed regularly.

One animal at a time was used for the testing of the heat resistance of the motor activity. The animal was put into Baltic sea water with a continuously increasing temperature (0.2°C/min, from 3–4°C to about 33°C), and its ability to right itself when turned on its back was tested at intervals of 5 min or less. The temperature at which the loss of the righting reflex occurred (critical thermal maximum, CTMax) and that of the cessation of pleopod beating were recorded. The locomotor activity/inactivity of the animals was also observed.

Stopwatch measurements of the beating frequency of pleopods were made at 4 and 14°C on animals turned on their backs, while they were quiescent. Three measurements were averaged for each animal and temperature.

In order to measure the thermal orientation behaviour of *Saduria*, a toroidal temperature gradient apparatus modified from that used by Tsukuda & Ogoshi (1985) was constructed. Flexible polythene tubing with a diameter of 5 cm forming a loop of length 95 cm was placed in a box, the ends of which were warmed and cooled either by means of a thermocontrolled water flow, or with an icebath. The depth of the Baltic sea water in the tubing was 2 cm, and the bottom of the tubing had a 0.5 cm deep layer of sand. Gradients of 2 to 17°C and 9 to 24°C could be reproduced and maintained. One animal at a time was put into the toroidal tubing through the hole in the middle

of the tubing. The walking track of *Saduria* was recorded manually on a chart for 10 minutes. This observation period was repeated at intervals of 30 min for 210 min. In the control experiments, *Saduria* moved in the apparatus at a uniform temperature of 4°C. Water temperatures on the gradient were measured with a 0.5 mm thermocouple inserted in the tubing through holes in its upper surface and read with an Ellab thermogalvanometer.

The statistical comparisons of the results were made using Student's *t*-test. The variation was expressed as the standard error of the mean (SEM).

3. Results

The results of the thermal behaviour and heat resistance experiments are given in Table 1. The temperature for the onset of inactivity of the locomotory behaviour when the temperature was increased from 4–5°C to about 33°C was not changed by temperature acclimation of the animals. No significant difference between the acclimation groups was found in the CTMax of the animals. However, a difference between the acclimation groups was observed in the temperature at which the beating of pleopods ceased. All these motor functions exhibited an adaptive change after seasonal warm acclimatization of the animals.

The mean pleopod beating rate of animals kept at 4°C was $49.9 \pm 1.8 \text{ min}^{-1}$ at 4°C, and $79.9 \pm 5.0 \text{ min}^{-1}$ at 14°C ($n=8$), and that of animals kept at

Table 1. Thermal behaviour and heat resistance of *Saduria entomon*. Mean temperatures (°C) for 6 animals \pm SE. For warm acclimatization, the animals were collected in the autumn at 13.5°C and kept at 13.1°C for 1–2 weeks.

Acclimation temperature and time	Temperature for the onset of inactivity	Temperature for the loss of righting reflex (CTMax)	Temperature for the cessation of pleopod beating
4°C, 1–2 weeks	15.2 \pm 0.7	26.4 \pm 0.5	30.8 \pm 0.2
14°C, 1 week	15.2 \pm 0.6	27.5 \pm 0.8	32.7 \pm 0.4**
14°C, 2 weeks	15.6 \pm 1.0	27.3 \pm 0.6	32.0 \pm 0.3*
4°C, 4 months	18.1 \pm 1.8	26.0 \pm 0.4	31.4 \pm 0.3
Warm acclimatization	21.6 \pm 1.0**	28.4 \pm 0.3**	33.0 \pm 0.2***

Significant difference from 4°C, 1–2 weeks: * $P<0.02$, ** $P<0.01$, *** $P<0.001$.

14°C was $46.2 \pm 2.3 \text{ min}^{-1}$ and $97.8 \pm 4.9 \text{ min}^{-1}$ ($n=6$), respectively. The difference at 4°C was not statistically significant but it was significant at 14°C ($P < 0.05$). The rate of pleopod beating thus exhibited inverse thermal acclimation at higher temperatures.

The positions of the animals in the thermal gradient apparatus was recorded for both gradients during the 6 observation periods of 10 min with intervals of 30 min. The final median of the temperature distribution of the animals was the same (15–17°C) in both gradients. Throughout the experiments the animals were distributed more evenly along the gradient extending from 9 to 24°C. The animals came to rest and often buried themselves in the sand within 30–120 min from the beginning of the experiment. This gave a measure of their selected temperature. The mean temperatures for this were $15.5 \pm 0.5^\circ\text{C}$ ($n=8$) along the 2–17°C gradient and $15.3 \pm 1.8^\circ\text{C}$ ($n=7$) along the 9–24°C gradient. These temperatures were not significantly different.

4. Discussion

The incipient upper lethal temperature for the antarctic giant isopod, *Glyptonotus antarcticus*, is about 6°C (Menzies & George 1968). *G. antarcticus* is an extreme cold water animal living at a nearly constant temperature of about -1.8°C . In general, the antarctic ectothermic marine fauna is considered highly stenothermic and evolutionarily cold adapted, as well as poorly capable of acclimatizing to a warm environment (Arnaud 1977, Clarke 1983).

The results of this study show that the heat resistance temperature of *Saduria* was much higher than the incipient upper lethal temperature of the antarctic isopod mentioned above. However, the poor acclimability of *Saduria*, found in the present study, is in agreement with the adaptation inability of the highly stenothermic animals like those found in the Antarctic. On the other hand, the poor acclimability of *Saduria* differs from the acclimability of eurythermic animals, i.e. animals living at a more or less fluctuating temperature. The ability of eurythermic animals to thermal acclimation is shown, for example, in the adaptive shift of the CTMax of crayfishes (Claussen 1980,

Kivivuori 1980, Layne et al. 1987) and of a freshwater isopod (Lagerspetz & Bowler 1989).

An ecologically valid temperature gradient should extend to the temperature at which the animal has been living. Our results from such a gradient, however, show that *Saduria* always selected a temperature about 10°C higher than their living temperature. This selected temperature range agrees with the temperature for the onset of locomotor inactivity of these animals observed in this study. The selected temperature of about 15°C in *Saduria* is within the same range found in the temperature selection of crayfish acclimated to 5°C (Kivivuori 1986). Ectothermic water animals tend in general to favour slightly higher temperatures than their "own" living temperature if this temperature is relatively low (Crawshaw 1975, Richards et al. 1977). It is possible that within a selected temperature range, the animal's abilities to seek food, grow etc., are at their thermal optimum. The neurophysiological basis of the temperature selection behaviour of these ectotherms is not known.

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