Vol. 47: 55–63, 1988

MARINE ECOLOGY – PROGRESS SERIES
Mar. Ecol. Prog. Ser.

Published July 21

Respiration, ventilation and circulation under hypoxia in the glacial relict *Saduria (Mesidotea) entomon*

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ABSTRACT: The glacial relict *Saduria (Mesidotea) entomon* (L.) (Crustacea: Isopoda) lives buried in sandy/muddy bottoms in the Baltic. During hypoxia *Saduria* remains buried until oxygen tension (P_wO_2) has decreased to < 5 Torr (8 °C; 7 ‰ S). Respiration rate ($\dot{M}O_2$) for buried *Saduria* was lower than for other crustaceans of similar size. *Saduria* is able to maintain a stable $\dot{M}O_2$ with decreasing P_wO_2 down to < 5 to 10 Torr, i.e. in practice over the entire P_wO_2 range. After exposure to severe hypoxia for many hours a respiratory overshoot was sometimes found. Only small amounts of haemolymph lactate had accumulated at $P_wO_2 = < 5$ Torr; up to 30 mg 100ml^{-1} after 144 h exposure. The presence of anaerobic endproducts other than lactate is suggested. Patterns of heartbeat frequency (f_h) and gill ventilation (f_g) changed considerably, but gradually, with time in buried *Saduria*. Normoxic f_h varied from 0 to 120 beats min^{-1} in a cyclic sequence lasting 5 to 6 min. f_g varied in a similar way although with different rates. At $P_wO_2 = < 10$ Torr the acute ventilatory response was a high stroke frequency, but after some hours the ventilatory pattern changed to the same cyclic sequence as at higher P_wO_2. f_h retained the same cyclic sequence in hypoxia as in normoxia but without cardiac arrests. Cardiac output remained constant over the entire P_wO_2 range but ventilatory efficiency increased with decreasing P_wO_2. Respiratory independence is governed by changes in ventilatory pump flow and in behaviour in order to facilitate the transfer of oxygen from the often hypoxic Baltic bottom water to respiratory tissues.

INTRODUCTION

The isopod crustacean *Saduria (Mesidotea) entomon* (hereafter *Saduria*) lives in muddy/sandy bottoms in the Baltic, the Bothnian Sea and in a few Swedish and Finnish freshwater lakes. Additionally it has a circumpolar distribution in the Arctic Sea. The uneven distribution, coupled with the geological history of the Baltic, is the reason for regarding *Saduria* as a glacial relict. The species is a scavenger and is an important component of the Baltic benthos, both as a consumer and as a food item for cod (Haahtela 1962).

Saduria is normally totally buried in the bottom substratum and emerges for feeding, reproduction and migration (Zmudziński 1966). It is a cold-water species, tolerating maximum temperatures of 12 °C but with its greatest biomass in the Baltic at temperatures as low as 2 to 3 °C (Mulicki 1957, Kopacz & Wiktor 1986). The buried mode of life, with no 'channels' or other connections to the sediment surface, exerts a special demand on the animal's ability to transport oxygen from the water above the sediment to the gills. Low dissolved oxygen concentrations are frequent and, in some areas, a permanent phenomenon in Baltic deeper waters (e.g. Mattäus 1983). The presence of hypoxia means an even greater demand on the ability of *Saduria* to extract oxygen from the water through the pore system in the sediment. Maintenance of respiratory level independent of water oxygenation is thus dependent on the ability to circulate oxygen in the body and on an effective transfer of oxygen through the gills and to/from blood pigment. Altered behaviour, such as emergence from the substratum, could also improve oxygen availability.

Tolerance tests to combinations of temperatures, salinities and oxygen concentrations are important for a basic understanding of the animal's reaction to environmental variables. Much of this basic knowledge is missing with regard to *Saduria*.

The purpose of this work was thus to determine the

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broad tolerance limits to certain environmental variables and to study the behavioural, metabolic, circulatory and ventilatory adaptations of *Saduria* to environmental oxygen deficiency.

MATERIAL AND METHODS

Specimens of *Saduria* were dredged in the Gulf of Gdańsk, Poland, at depths of >15 m. Upon return to the laboratories, the isopods were stored at their ambient salinity and temperature (S = 6 to 8 ‰; T = 5 to 8 °C).

Tolerance experiments were carried out in Gdańsk, Poland, and for respiratory and circulatory/ventilatory experiments, *Saduria* were transported to Helsingør, Denmark and stored there under the same conditions. They were fed twice weekly with fish meat.

Respiration experiments were performed according to Hagerman & Szaniawska (1986). The respiration chamber contained sufficient substratum (ignited fine sand) for *Saduria* to completely bury itself (disappear) in the sand. Oxygen tensions (P_wO_2) were kept constant by bubbling mixtures of N_2 and air through the water reservoir. The respiration chamber was covered with black plastic to reduce light intensity. Each individual was used only once.

Haemolymph samples for analysis of circulating lactate were taken by inserting a hypodermic syringe (Terumo, 100 µl) into the heart region of *Saduria*. Lactate was analysed using Boehringer Test Combination 124842. Blood samples were taken at the end of each respiration experiment. Separate experiments exposed a number of *Saduria* to either $P_wO_2 = 5$ to 10 Torr or to $P_wO_2 = <5$ Torr (1 to 3 Torr) for 144 h; lactate samples were taken daily. Each individual was sampled only once.

Ventilation and circulation activities were measured using an impedance technique. The outputs of impedance pneumographs were connected to a Goerz Servogor SE 220 2-channel recorder. For recording of heartbeat frequency (f_h), a thin, shellac-covered copper electrode (diameter 0.15 mm) was mounted on the posterior edge of the penultimate thoracic segment. For recordings of pleopod ventilation frequency (f_g), a similar copper electrode was mounted on the inner edge of one of the ventral lids covering the abdominal gill chamber. The electrodes were fastened with 'superglue' (UHU-Instant). *Saduria* was always left for ca 3 h to recover after electrode mounting. For simultaneous recordings of ventilatory and circulatory activity and respiration rate ($\dot{M}O_2$; ml O_2 g^{-1} h^{-1}), the electrodes connecting wires were taken out through a small hole at the top of the respiration chamber. This hole was made impermeable to oxygen with silicone. The placement of the f_h and f_g electrodes on the specimen in the respiration chamber is shown in Fig. 1. The thin electrode wires did not prevent the isopods from swimming or from burying in the sediment. All experiments were performed at 8 to 10 °C. Recordings of $\dot{M}O_2$, f_h and f_g were made for up to 72 h for any individual.

RESULTS

Salinity/temperature tolerance

Tolerance experiments to salinity/temperature combinations (0 to 30 ‰ in 5 ‰ intervals; 5 and 10 °C) showed *Saduria* to be an extremely euryhaline organism. LT_{50} in 0 ‰ was 20 d at both temperatures, and survival was 100 % over the same period in the rest of the salinity range, except at 30 ‰ where LT_{50} was 20 d at 5 °C and 18 d at 10 °C. At the extreme salinities (0 and 30 ‰) the isopods did not bury in the sediment during the first day.

Behaviour during exposure to hypoxia

Under normoxic conditions *Saduria* is totally buried in the substratum and emerges only for foraging and migration. In the storage aquaria no *Saduria* were normally seen, but as soon as food was given all individuals emerged and crawled towards it. At a moderate hypoxia of 40 Torr the tip of the abdomen was usually seen at the surface of the muddy sand. When P_wO_2 was further decreased to 25 Torr, *Saduria* emerged slightly so that the whole abdomen was above the substrate. It remained in this position until P_wO_2 was lowered to 5 Torr and then emerged totally. If P_wO_2 was increased slightly, to 15 Torr, *Saduria* immediately partly buried again so that only the abdomen was visible. In this way it was possible to keep the specimens inside or out of the substratum by slight changes of the oxygen tension. The different behavioural reactions to various P_wO_2 did not change with time; for instance even if a P_wO_2 of 25 to 30 Torr prevailed for several hours *Saduria* did not emerge completely.

Respiratory rate ($\dot{M}O_2$) during normoxia and hypoxia

$\dot{M}O_2$ of *Saduria* under normoxic conditions and when buried in the sand is shown in Fig. 2. $\dot{M}O_2$ was very low; an individual of 2 g (wet wt) respired 0.08 ml O_2 g^{-1} h^{-1}, an individual of 1 g respired 0.13 ml O_2 g^{-1} h^{-1}. Corresponding rates for specimens not buried in the sand and of similar sizes were 0.25 and 0.5 ml O_2 g^{-1} h^{-1} respectively. During normoxia no diel rhythmicity

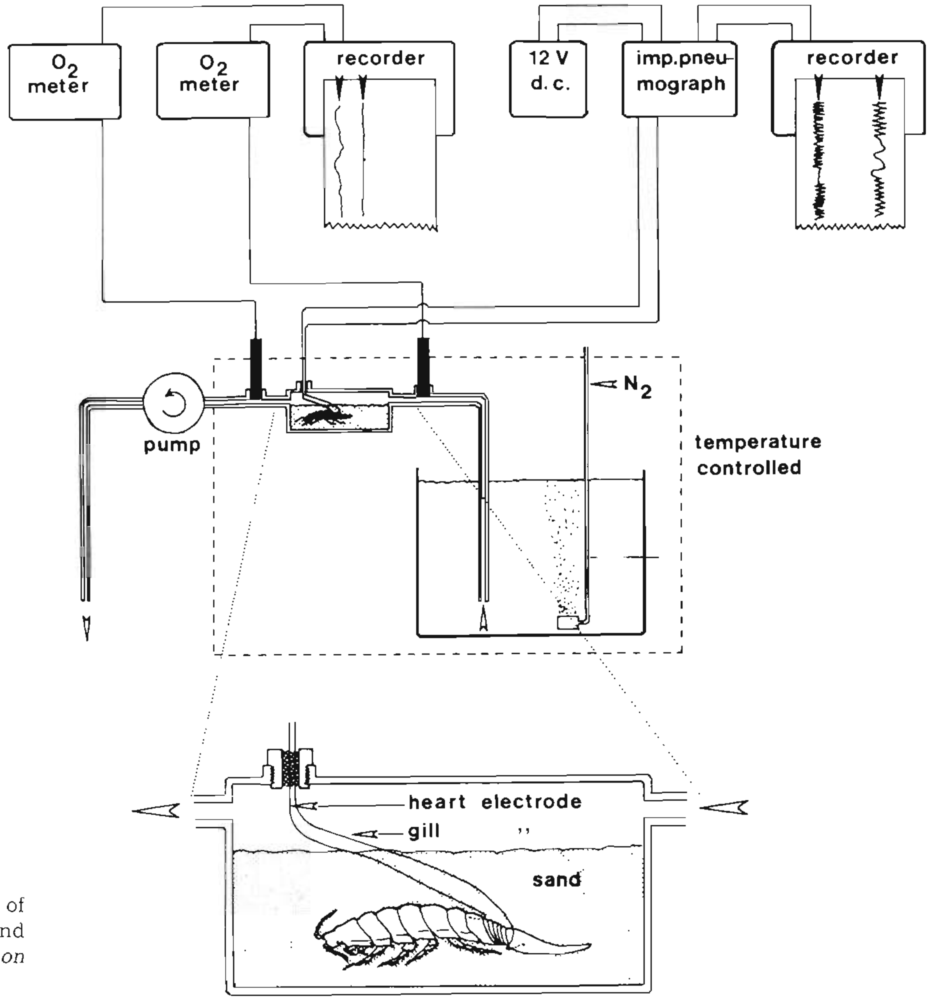

Fig. 1. Experimental setup and sites of implantation and fastening of heart and pleopod electrodes on *Saduria entomon* in the respiration chamber

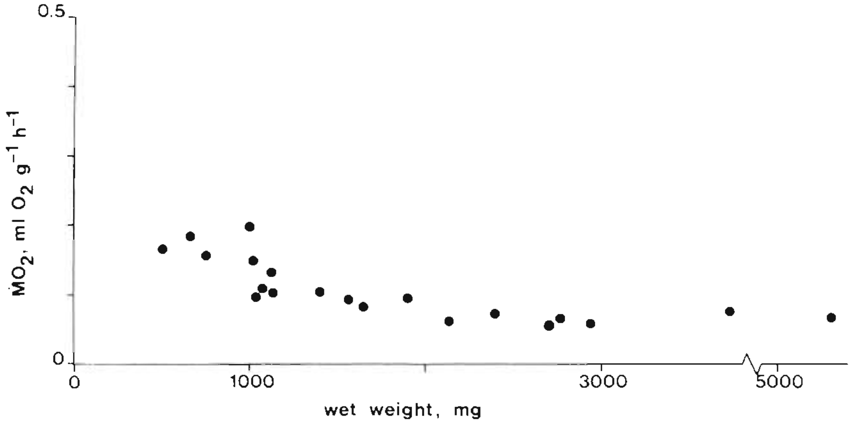

Fig. 2. *Saduria entomon*. Normoxic respiration rate ($\dot{M}O_2$) as a function of wet weight for buried, quiescent isopods (8 °C; 7 ‰)

in $\dot{M}O_2$ was evident; as enough sand was available in the respiration chamber the isopods remained buried and inactive during normoxic respiration experiments. Fig. 2 shows that $\dot{M}O_2$ altered little with body size.

During hypoxia, *Saduria* was able to maintain its $\dot{M}O_2$ level (Fig. 3) down to a P_wO_2 of 10 to 15 Torr (i.e. less than 10 % oxygen saturation). This regulatory ability was independent of body size. This so-called P_c, i.e. the point where *Saduria* can no longer maintain its $\dot{M}O_2$ independent of P_wO_2, is so low that in practice *Saduria* can extract all oxygen from the water.

Even during prolonged exposure to severe hypoxia

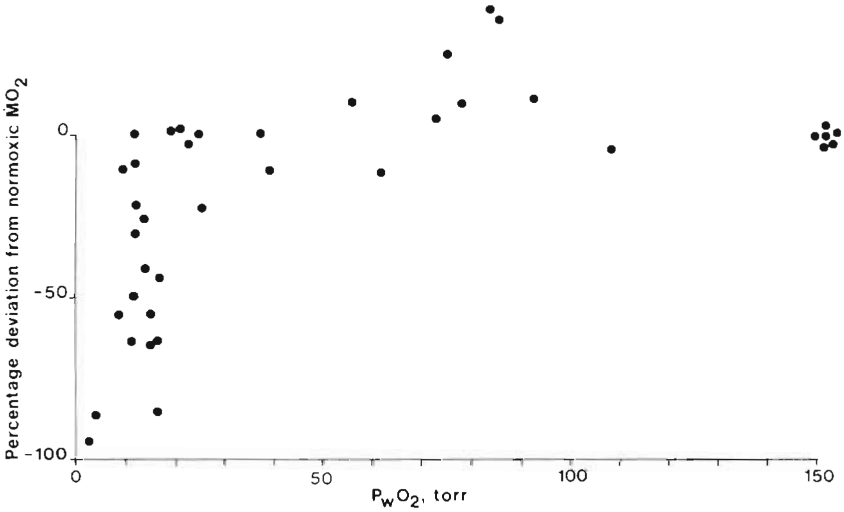

Fig. 3. *Saduria entomon.* $\dot{M}O_2$ as percentage deviation from the normoxic $\dot{M}O_2$, in relation to the oxygen tension of the water (8 °C; 7 ‰)

(P_wO_2 = 20 Torr for up to 72 h) *Saduria* maintained its $\dot{M}O_2$ constant, with only small irregular variations and with the behavioural changes caused by the low oxygen content (see above).

Respiratory overshoot after a period of hypoxia

If oxygen supply is insufficient for metabolic needs, an animal reverts to anaerobic metabolism, and when oxygen supplies become sufficient again then an enhanced oxygen uptake from the medium occurs (i.e. a respiratory overshoot which is used for reoxidising the various anaerobic endproducts). Such an oxygen debt was also seen in *Saduria* when it was exposed to P_wO_2 = < 15 to 30 Torr for periods of 3 h and longer. However, this overshoot did not always occur; in some experiments even at very low oxygen tensions no respiratory overshoot was seen at all. Fig. 4 gives an example of a respiratory overshoot in normoxia after an exposure to P_wO_2 = 15 Torr for several hours. The increase in $\dot{M}O_2$ upon return to normoxic conditions varied between 1.6 and 2.2 times the normoxic $\dot{M}O_2$ ($n = 7$). The magnitude of the overshoot seems to be independent of the length of the hypoxia experienced.

Lactate accumulation during hypoxic exposure

As a result of anaerobic metabolism crustaceans normally produce lactate which accumulates in the haemolymph (Bridges & Brand 1980). A basic, normoxic blood lactate level of < 10 mg $100ml^{-1}$ was observed in *Saduria* (Fig. 5A) and this increased only slightly when P_wO_2 was decreased even to extremely low values: lactate was ca 30 mg $100ml^{-1}$ at P_wO_2 = 1 Torr. This small increase is also seen when lactate is plotted against time for P_wO_2 < 10 Torr (Fig. 5B). At 5 to 10 Torr, lactate remained at normoxic levels during the whole experiment (144 h). After 24 h at < 5 Torr, lactate increased from the basic ca 10 mg $100ml^{-1}$ to ca 25 mg $100ml^{-1}$ and stayed at this level for at least 144 h. This slight increase shows that a possible anaerobic metabolism, indicated by the respiratory overshoot mentioned earlier, must have produced endproducts other than lactate.

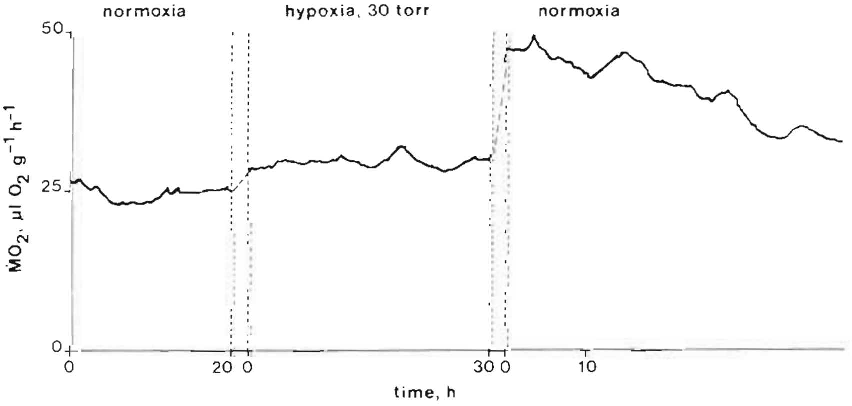

Fig. 4. *Saduria entomon.* Example of $\dot{M}O_2$ at normoxia, severe hypoxia and again normoxia showing respiratory overshoot (8 °C; 7 ‰)

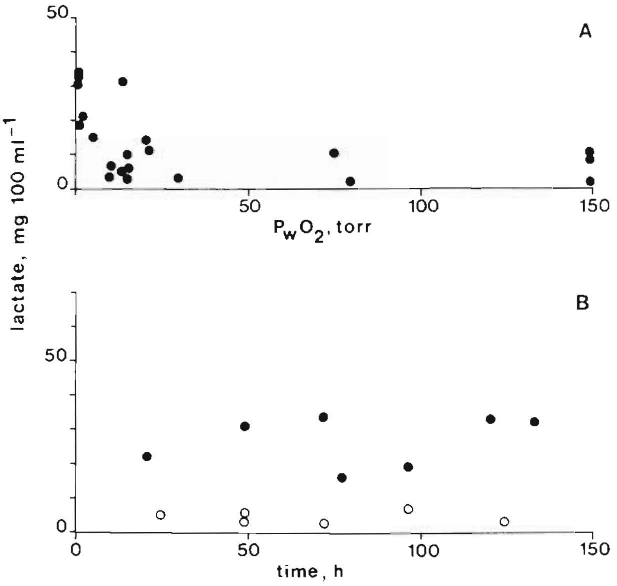

Fig. 5. *Saduria entomon*. (A) Haemolymph lactate accumulation when exposed to various oxygen tensions (P_wO_2). (B) Haemolymph lactate accumulation as a function of time when exposed to P_wO_2 = 5 to 10 Torr (○) and < 5 Torr (●) (8 °C; 7 ‰)

Ventilation (f_g) and circulation (f_h) rates

The heart of *Saduria* is tubular and slender and situated in the abdomen just anterior to the pleotelson. The anterior aorta continues as an anterior prolongation of the heart. The heart extends into posterior and lateral arteries directly connected to the pleopods which are used for both swimming and as gills. As is typical for valviferan isopods, the pleopods are covered by a pair of lids formed from the last pair of pleopods.

The pattern of gill ventilation and heart rate changed considerably with time and with experimental conditions and was complicated by the different functions of the pleopods: more or less intermittent respiratory movements with or without the lids and swimming movements by the pleopods alone. Basic, normoxic patterns of f_g and f_h for quiescent, buried *Saduria* are shown in Fig. 6A and B. Normoxic f_h for the totally buried isopod varied from 0 to 120 beats min^{-1}. Ventilation frequency varied in a similar way although with different rates. The lowest normoxic f_g measured was 20 beats min^{-1}. Rate changes for both organs were slow and gradual. However, low beat rates of either organ were often associated with a higher beat amplitude, suggesting a higher pump stroke volume. This means that the output (f × stroke volume), as seen from Fig. 6, was almost the same per time unit even if the rate changed.

Under normoxic conditions the heart ceased beating for up to 24 s. When it started beating again the rate was very low but amplitude was high. Later, maximum frequencies occurred and then rates gradually decreased again to a new arrest. Such a cycle took about 5 to 6 min; f_g was not observed to stop totally but showed a similar pattern of altering beat frequency.

At moderate hypoxia (55 Torr), when the isopod is still buried, the same type of cyclical sequences prevail for both f_h and f_g but both amplitude and frequency may be slightly modified.

At very low oxygen tensions (< 10 Torr) the acute ventilatory response was a high stroke frequency (up to 240 beats min^{-1}) but with a much lower amplitude (Fig. 7). After several hours in the low P_wO_2 *Saduria* seemed to adapt to the new tension (and may even bury itself again) and the ventilatory pattern changed to the same cyclic sequence as seen at higher P_wO_2, but with amplitude and frequency generally still higher than during normoxia. Heart activity retained the cyclic sequences during hypoxia but no cardiac arrests were seen at these low P_wO_2 values.

Ventilation and circulation outputs can be compared using the product of beat amplitude and beat frequency for fixed time intervals and for different P_wO_2 values and during different ventilatory and circulatory patterns. When percentage deviations from normoxic levels are compared (Fig. 8A and B) it is clear that the heart output remained constant over the P_wO_2 range analysed, i.e. a constant cardiac output per unit time. Ventilatory performance (i.e. the transport of water over the pleopods) showed an increase with decreasing P_wO_2. This increased performance was further facilitated by the behavioural changes in the isopod. At high and moderate P_wO_2, the availability of oxygen in the sediment is enough for *Saduria*'s metabolic needs and compensation where needed is achieved by merely altering heart or ventilation amplitude or frequency periodically. At P_wO_2 = 40 Torr, *Saduria* sometimes raised the tip of the abdomen above the sediment as the availability of oxygen in the sediment was too low. At still lower P_wO_2 (5 Torr), *Saduria* emerged totally and increased the availability of oxygen by rapid simultaneous pumping of all pleopods and by opening/closing of the lids. The respiratory independence is largely governed by changes in ventilatory pump flow and only to a very minor degree by the circulatory output, which remains relatively constant over the P_wO_2 range tested.

DISCUSSION

The $\dot{M}O_2$ for *Saduria* measured here is considered to be a 'resting' metabolism, and periodically a 'routine' metabolism, i.e. when the animal moves a little in the sand. The values are low compared with those of other

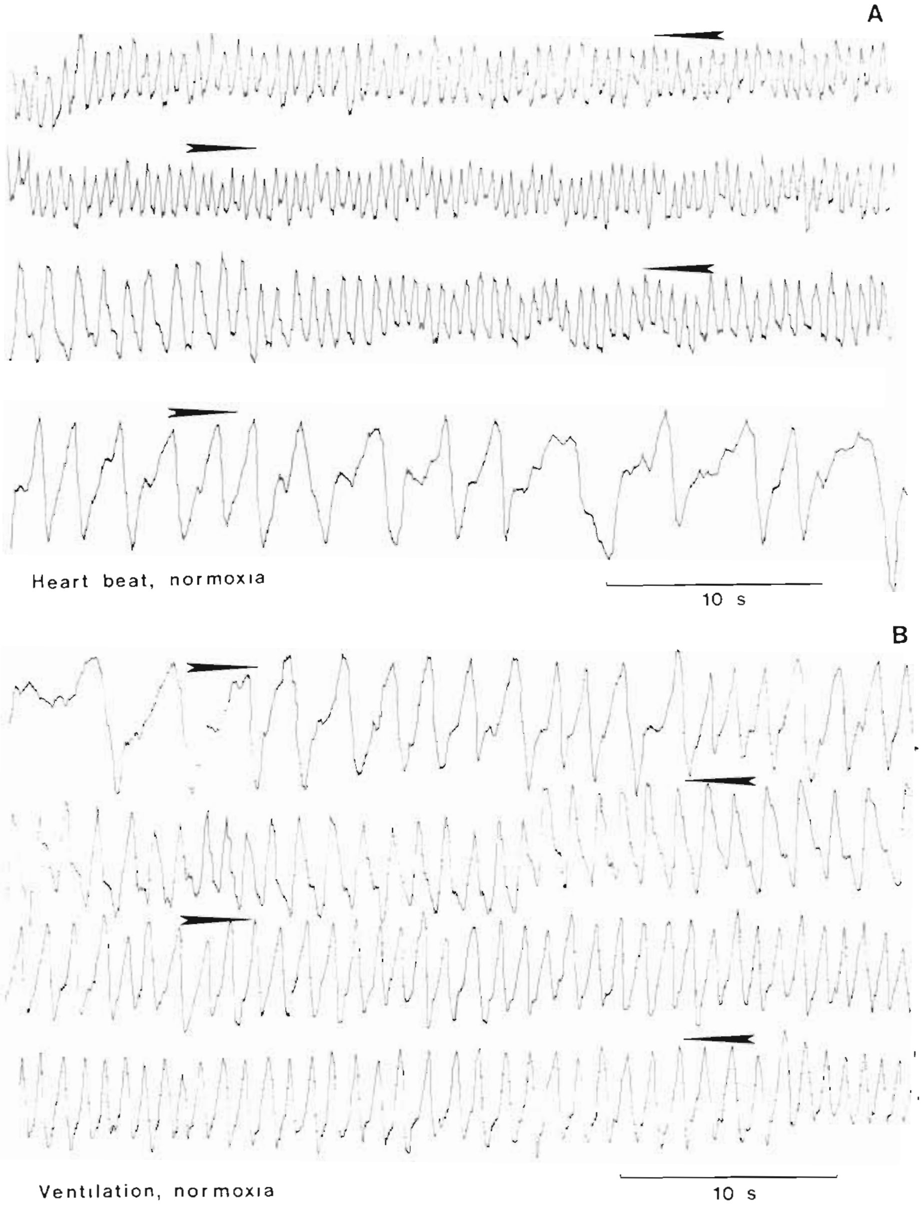

Fig. 6. *Saduria entomon.* Example of typical changes in heart frequency (A) and pleopod ventilation (B) with time in normoxia for a quiescent, buried isopod (8 °C; 7 ‰). Arrows show in which direction to read the recording trace

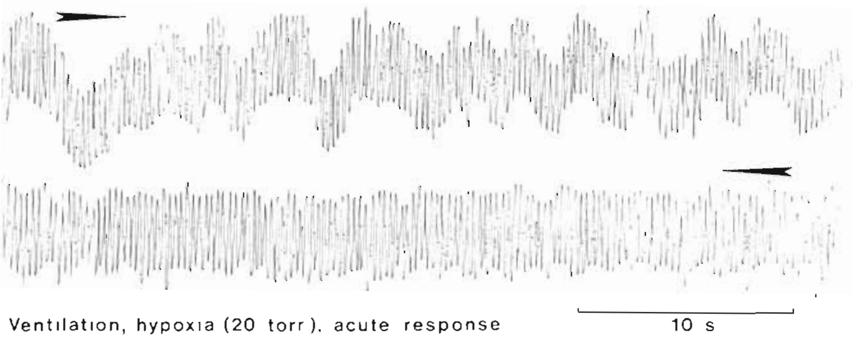

Fig. 7. *Saduria entomon.* Acute response of ventilation (pleopod beating) upon exposure to hypoxia of < 5 Torr (8 °C; 7 ‰). Arrows show in which direction to read the recording trace

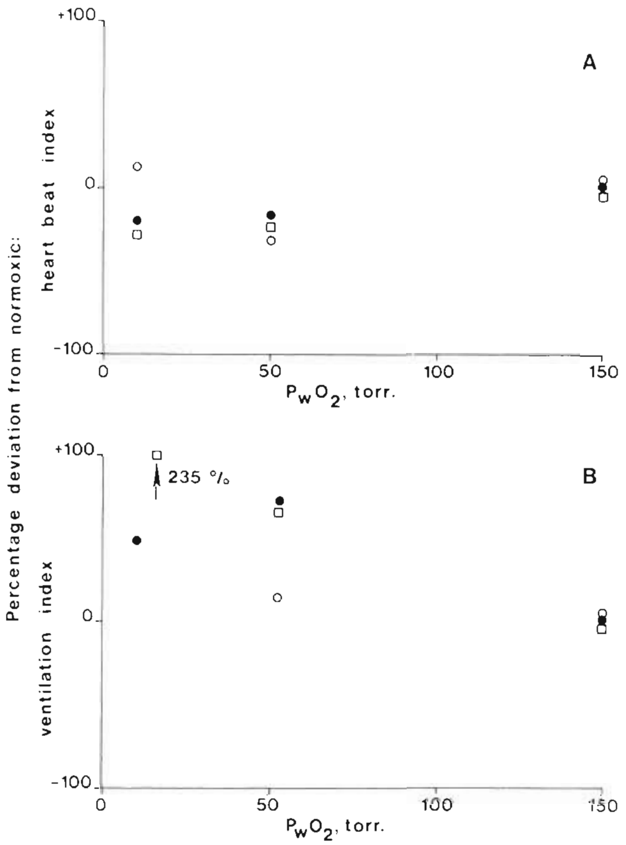

Fig. 8. *Saduria entomon*. 'Efficiency' (product of amplitude and frequency) of (A) heart and (B) ventilation calculated during 3 different periods of a sequence (see text for further explanations) and at 3 different oxygen tensions (8 °C; 7 ‰). (○) Low organ frequency; (●) mean organ frequency; (□) high organ frequency

crustaceans of similar size (Waterman 1960, Newell 1979, McMahon & Wilkens 1983). *Saduria* lives a very inactive life in the sediment and, being a scavenger, is active only when food is found. Burrowing crustaceans have metabolic rates that are usually lower than non-burrowing species (Bridges & Brand 1980, Hagerman & Uglow 1985). Kangas & Lappalainen (1978) measured the $\dot{M}O_2$ of *Saduria entomon* from the Gulf of Finland using a closed respiratory system and without the provision of substratum in the chamber, and obtained values considerably higher than those found here. It has however been shown that the presence of sediment can decrease $\dot{M}O_2$ (Bridges 1976, Hagerman & Szaniawska 1988).

The $\dot{M}O_2$ of *Saduria* is independent of P_wO_2 at least down to 10 Torr (i.e. in practice over the entire possible P_wO_2 range). Such an ability is partly an effect of favourable experimental conditions (Hagerman & Szaniawska 1988) but also indicates an ability to utilize the, often very low, oxygen content in Baltic bottom waters (Mattäus 1983). It was not possible to clearly identify a P_c value because *Saduria* often used all the oxygen available in the flow-through system.

The absence of a diel rhythmicity of $\dot{M}O_2$ in *Saduria*, compared with, for instance, the shrimp *Crangon crangon* (Hagerman & Szaniawska 1988) is certainly due to the stable environmental conditions which prevail at the bottom. Instead, activity patterns are governed by intermittent supply of food (Haahtela 1978).

Respiratory overshoot after hypoxic periods has been reported for many crustaceans (e.g. thalassinid mud shrimps; Thompson & Pritchard 1969) and is generally considered to represent repayment of oxygen debt. It is difficult in the present instance to make any quantitative estimations of this. Presumably oxygen debt occurs under conditions where anaerobic endproducts accumulate and re-oxidation of these is reflected in the $\dot{M}O_2$ immediately after a period of severe hypoxia/anoxia.

Anaerobic endproducts usually accumulate only where $P_wO_2 < P_c$ (Bridges & Brand 1980). The ability of *Saduria* to utilize all available oxygen (= absence of P_c) is thus further reflected in the low lactate concentration that accumulates in the haemolymph even after more than 100 h exposure to $P_wO_2 = < 5$ Torr. Lactate is the normal anaerobic endproduct in crustacean carbohydrate metabolism and crustaceans generally accumulate lactate to much higher concentrations (Albert & Ellington 1985) and survive much shorter periods of hypoxia (Bridges & Brand 1980) than shown by *Saduria*. The possibility exists that *Saduria* has an alternative anaerobic endproduct, as is indicated by the respiratory overshoot that sometimes occurs. Carbohydrate metabolism in isopods under severe hypoxia is not especially well documented. Succinate and alanine have been found in small amounts under environmental anaerobiosis in the scavenging isopod *Cirolana borealis* while up to 50 % of the produced lactate was excreted (de Zwaan & Skjoldal 1979). The horseshoe crab *Limulus polyphemus* accumulates arginine and alanine as well as lactate in muscle and hepatopancreas during anaerobiosis (Carlsson & Gäde 1986). As *Saduria* is a primitive crustacean, compared to the better-documented decapods, it is reasonable to assume that anaerobic endproducts commonly found in annelids and molluscs might also appear in *Saduria*. Further investigations within the present programme will test this.

Studies of circulatory and ventilatory activities have, to our knowledge, not so far been made on isopods, although decapods are fairly well-investigated (McMahon & Wilkens 1983). However, it can be stated that the simple, tubular heart of isopods beats by a temporal sequence of muscle contractions (Needham 1954). In decapods, the heart normally beats with constant frequency and amplitude; cardiac arrests, bradycardia and tachycardia are sudden and then remain constant once they have taken place (e.g. Cumberlidge & Uglow 1977), whereas gradual changes in both amplitude and frequency seem to be a normal feature for *Saduria*. The decapod heart reacts immediately to external stimuli (Florey & Kriebel 1974) but *Saduria* hearts seem to continue their cyclical beating regardless of external variables. The cardiac arrests that occur in normoxia and moderate hypoxia are thus normal events in the beat cycle: slower and slower until total stop, then gradually starting again.

Heart and ventilatory behaviour seem to be closely correlated. This is reasonable, firstly because the heart is situated in the abdomen very close to the pleopods, and secondly because data for must crustacean groups seem to indicate a common neural coordination system (McMahon & Wilkens 1983). This coordination is complicated in isopods by the double function of the pleopods: for both oxygen uptake and for swimming. A synchronous beating of the pleopods is as normal as an asynchronous beating, but water transfer is presumably much more efficient during synchronous beating. Thus, when calculating the 'pump efficiency' it is necessary to use longer time intervals, and when doing so, it is obvious that the increased ventilation efficiency during hypoxia is similar to the increased scaphognathite beating in decapods under hypoxia (Hagerman & Uglow 1985). In decapods cardiac output also increases under hypoxia (McMahon & Wilkens 1983) but the 'heart pump efficiency' of *Saduria* is constant with decreasing P_wO_2.

Thus, the possibility of maintaining $\dot{M}O_2$ independent of P_wO_2 over practically the entire P_wO_2 range is governed mainly by the increased efficiency of water transfer over the pleopods. In the sediment, the transport of water through the interstitial pore system must be slow and the changed behaviour of *Saduria*, i.e. the emergence response at very low P_wO_2, will increase the availability of O_2 by effecting access to greater amounts of water.

Saduria has a haemocyanin and a haemolymph oxygen carrying capacity comparable to those of active and burrowing decapods (Hagerman & Oksama 1985). When *Saduria* is inactive in the sediment and with a very low $\dot{M}O_2$, the amount of haemocyanin and its characteristics are less important as, even under severe hypoxia, it is still possible for *Saduria* to obtain most of the oxygen necessary from the water. However, during active periods in hypoxia, as when food is supplied and the cardiac output remains constant, *Saduria* is dependent on a high oxygen-carrying capacity for the transport of oxygen to the relevant tissues. If the active period is prolonged or the hypoxia changes to anoxia, *Saduria* will have to change to anaerobic metabolism.

Acknowledgements. This work was supported by the Danish Science Research Council.

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This article was presented by Professor E. Naylor; it was accepted for printing on May 16, 1988