

## Hypostenothermic organisms

### 1. Introduction

The object of this study is to discuss the results of investigations carried out to establish, (1) upper lethal temperatures of, (2) to determine respiratory responses to a rise in temperature, and (3) relationship between respiration rate and body weight of ectothermic animals living normally at stable sub-zero temperatures. This kind of environment is found in the coastal waters of Antarctica.

Within the whole area of Antarctica the temperature of the surface water layer down to the depth of about 200 m deep ranges from  $-1.8^{\circ}$  to  $4.0^{\circ}$  (Kort 1969). In the Antarctic Convergence the water temperature rises suddenly by  $5^{\circ}$ — $8^{\circ}$  and makes a natural barrier (cf. Brodskij). The temperature of the shelf waters near the Continent ranges from  $-2.2^{\circ}$  to  $-1.5^{\circ}\text{C}$  (Littlepage 1965, Rakusa-Suszczewski 1972a). The area with such temperature conditions are thousands of  $\text{km}^2$ .

Under natural conditions a long-lasting super-cooling of sea-water is not possible. The freezing temperature of sea-water at a given salinity is sharp, below which a series of substantial changes occur in the water environment, such as: increase in salinity, changes in conductivity, solubility of gases etc. Thus, the relationship between organisms, under such environmental conditions, and temperature may be represented asymmetrically (Fig. 1). This

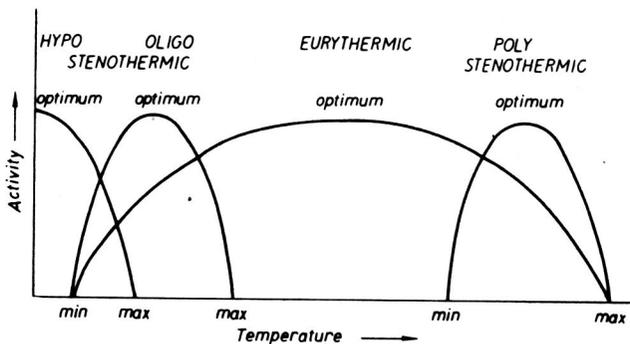


Fig. 1. Comparison of the relative ranges of tolerance of stenothermic (oligo- and poly-) and eurythermic organisms (Rutter 1953)

The term "hypostenothermic" applies to organisms adapted to the environment with sub-zero temperatures and very slight fluctuations at the border of the freezing point of the sea-water.

supplements Ruttner's (1953) classification of aquatic organisms in relation to environmental temperatures, with an additional group which we propose to call: hypostenothermic organisms, the lowest temperature nearest to the freezing point of the seawater should be optimal for these organisms. In our opinion, this is expressed consistently by the proposed diagram and confirmed by results from experimental studies.

## 2. Upper lethal temperature

There is not much information concerning high temperature resistance and survival of ectothermic organisms living at sub-zero temperatures. Armitage (1962), studying respiration of the amphipoda *Orchomonella chilensis* in an acute experiment observed high mortality at 12°C. *Paramoera walkeri* (Amphipoda) acclimated at temperature range from -1.2° to 12°C (7-10 days was spent at each temperature which was then increased in 2.0°C steps) showed high mortality among individuals at 10°C, Rakusa-Suszczewski and Klekowski (1973). According to George (1971) the upper lethal limit for the Antarctic species *Glyptonotus acutus* is 2° or 3°C. The studies of Rakusa-Suszczewski (in prep.) on the amphipod, *Orchomene plebs* (probably the same species examined earlier by Armitage (1962) as *O. chilensis*) gave an LD<sub>50</sub> in the range of 7-8°C. As in *Paramoera walkeri* earlier stages of the life cycle of this species show the lowest sensitivity

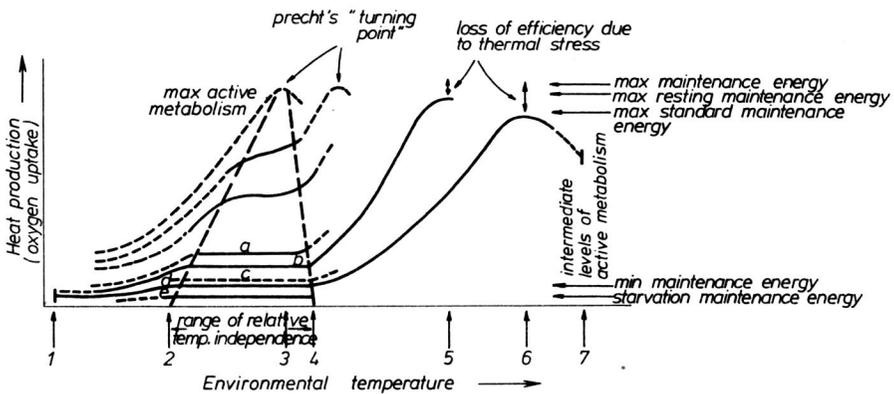


Fig. 2. The effect of temperature on heat production (oxygen consumption in poikilothermic organisms after Duncan and Klekowski 1975)

At the level of standard metabolism changes in the adaptation — dependent range of temperatures do not cause any changes in oxygen consumption. In the state of active metabolism every change in temperature causes a decrease in oxygen consumption. The highest oxygen consumption occurs at the optimum temperatures for the animal species. 1 — lower lethal temperature, 2 — lower critical temperature, 3 — temperature of maximum activity, 4 — upper critical, 5 — temperature of maximum resting metabolism, 6 — temperature of maximum standard metabolism, 7 — upper lethal temperature: a) routine metabolism and specific dynamic action, b) routine metabolism, c) standard metabolism and specific dynamic action, d) standard metabolism, e) starvation metabolism.

to higher temperatures. Belman and Giese (1974) in their studies on respiration of *Sterechinus neumayeri* (Echinoidea) and *Odonaster validus* (Asteroidea) found that animals at 5°C “became flaccid and eventually died”. The lethal temperature for the Antarctic fish *Trematomus* sp. is at about 6°C (Somero and DeVries 1967).

In experimental studies on respiration, oxygen consumption rates may be used as a criterion for determination of optimal temperature conditions for respiration of animals. This is shown in Fig. 2, where a scheme for the effect of temperature on respiration of ectotherms, as proposed by Duncan and Klekowski (1975) is presented diagrammatically. This is constructed from relevant investigations and observations. As can be seen in Fig. 2, there exist temperatures at which the oxygen consumption range is widest ( $T^{\circ}$  of max. activity). In cases of temperatures higher or lower than “optimum” for the animal, at a state of maximal activity, oxygen consumption falls.

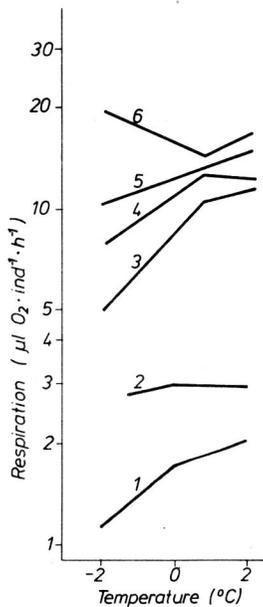


Fig. 3. Effect of temperature on antarctic amphipod respiration

1 — Phytophagous *Paramoera walkeri*, 35 mg wet weight, acute experiment, in winter (Klekowski, Opaliński and Rakusa-Suszczewski 1973), 2 — *P. walkeri*, 35 mg wet weight, 7—10 day acclimation to temperatures of 0° and 2° (Rakusa-Suszczewski and Klekowski 1973), 3 — *Orchomene plebs*, co 100 mg wet weight, acute experiment, starved animals, 4 — *Orchomene plebs*, calculation from regression for a 100 mg wet weight individual, 7—10 day acclimation to temperatures of 1° and 4° (Rakusa-Suszczewski, in prep.), 5 — *Orchomonella chilensis*, calculation from regression for a 100 mg wet weight individual, acute experiment (Armitage 1962), 6 — *Orchomene plebs*, co 100 mg wet weight, acute experiment, active animals (fed) (Rakusa-Suszczewski, in prep.). Animal reaction to temperature depend on the level of metabolism in the organism at the lowest temperature corresponding to the environmental conditions. The greatest in oxygen consumption occur at the lowest temperature. The effect of temperature changes on organisms with a low level of metabolish causes a very strong reaction.

Standard metabolism is not affected by temperature in a given range (thermic independence zone). Above the upper critical maximum temperature respiration rate increases (Fig. 2), or decreases at the level of maximal active metabolism. Consequently the oxygen consumption range between the lowest and the highest level of metabolism is narrower.

In animals living at varying temperatures the ability to maintain a temperature independent zone of respiration, is taken to infer the presence of energy-saving mechanisms. This has been observed by Belehradek (1935), Stroganov (1956), Wieser (1973) and other authors. The effect of temperature on respiration of some *Crustacea* from Antarctic waters is shown in (Fig. 3). As can be seen the range of oxygen consumption of the three species are widest at the lowest temperature corresponding to that of the habitat. Animals exposed to temperatures higher than environmental by 2°—3°C showed a decrease in oxygen consumption and the range between the lowest and highest level is narrower than at sub-zero temperatures. This can be seen also from (Fig. 4).

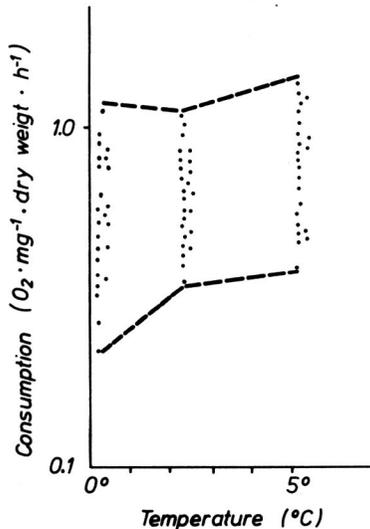


Fig. 4. Responses in oxygen consumption of *Euphausia superba* to temperatures of 0° and 2° immediately after collection from sea water at temperatures of -0.9° and -1.27° and after 4 days, following the sampling at 2°C (after McWhinnie and Marciniak 1965 with modifications)

Belman and Giese (1974) investigated the effect of temperature on respiration of *Strechinus neumayeri* (*Echinoidea*) and *Odontaster* (*Asteroidea*) after 3-days acclimation at temperatures ranging from -1.8 to 3.0°C. No significant differences were found in oxygen consumption rates of both species at the examined range of temperatures. If the results obtained by Belman and Giese (1974) for *Odontaster validus* were converted into dry weight, which constitutes about 20% of wet body weight in this species (Dayton et. al. 1974), oxygen consumption would amount to 24.5 ml O<sub>2</sub> · kg<sup>-1</sup> · h<sup>-1</sup>.

According to Dayton et al. (1974) oxygen consumption of *Odonaster validus* at  $-1.8^{\circ}\text{C}$  is lower and only amounts to  $10.14 \text{ ml O}_2 \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$ . Belman and Giese (1974) therefore have examined individuals with a high metabolic rate, so they did not observe the effect of higher temperature ( $3^{\circ}\text{C}$ ) on oxygen consumption rates. It is an analogous reaction to that noted in the *Crustacea* (Fig. 3), which were at the level of routine or close to the active metabolic rate at the lowest temperature.

Papers treating the effect of temperature on respiration of Antarctic fish are very numerous but only some are relevant to this discussion. The results of Wohlschlag (1960, 1963) concerning respiration of *Trematomus bernacchii* and *Rhigophila dearborni* (Fig. 5 and 6) corroborate our observations that in fish also the oxygen consumption range is widest at the lowest temperature and even a slight rise in temperature by  $2^{\circ}$ – $3^{\circ}\text{C}$  limits the range (scope) of oxygen consumption distinctly. A comparison of results from the papers by Gordon, Robilliard and Dayton (1969) and Hemmingsen, Douglas and Grigg (1969) concerning a respiration of *Pagetopsis macropterus* (*Chaenichthyidae*) similarly indicates a very wide range of oxygen consumption from  $14.7$ – $29.3 \text{ mg O}_2 \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$  and  $34.5$ – $86.9 \text{ mg O}_2 \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$  at a temperature of  $-1.8^{\circ}\text{C}$ .

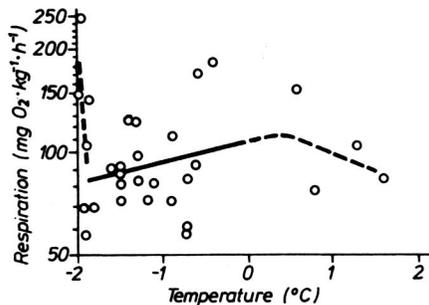


Fig. 5. *Trematomus bernacchii* metabolism-temperature plot

Solid line has slope of  $0.06 \text{ log} \cdot \text{mg O}_2$  consumed per h per kg for each degree centigrade increase in temperature. Broken lines indicate possible deviations from linearity at the temperature extrem (Wohlschlag 1960).

So, range of oxygen consumption by animal can be considered as an indicator for identification of most favorable thermal conditions for it. For Antarctic animals this is the lowest temperature of sea water. Organisms in a state of low activity subjected to temperatures only slightly higher ( $1^{\circ}$ – $2^{\circ}$ ) than in the environment show increases in respiration rate with high  $Q_{10}$  values (cf. Fig. 2). This kind of reaction is characteristic of organisms exposed to temperatures above the upper critical limit. It seems that animals living under sub-zero temperature conditions are unable to maintain respiration rates at a constant level. In this manner, animals living at constant temperatures show a lack of adaptation and lack of the energy conserving mechanisms, as it is for animals living in varying temperatures. This may be reason for widening of the range of the oxygen consumption in hyposten-

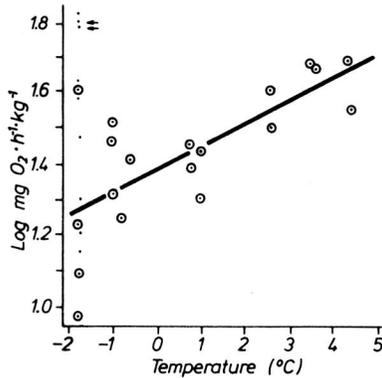


Fig. 6. *Rhigophila dearborni* metabolism-temperature relationship

Circled points based on 3-hour determinations. Other points based on 45 min. determinations. Arrows indicate metabolic level of 2 immature fish weighing 10 g each (Wohlschlag 1963). At the lowest temperature the oxygen consumption range is the widest.

thermic organisms, as compared with oligostenothermic and eurythermic animals.

Summing up, it may be said that the upper lethal temperature occurs between 5°—8°, and the widest range of oxygen consumption being at the lowest sub-zero temperature makes the relationship between biological processes of animals living under such conditions and the temperature is possible to express asymmetrically (Fig. 1).

### 3. Relationship between oxygen consumption and body weight

Correlation between respiration of animals and their body weight is significant especially in comparative studies. This relation may be expressed in the double logarithmic plot by the formula  $R = aW^b$ , where  $R$  — oxygen consumption,  $W$  — body weight,  $a$  and  $b$  — constant coefficients. At the low temperatures prevailing body weight increases very slowly, life cycles are very long and reproduction is often restricted to a very short summer season. In a population, two, three or more generations may be observed to preserve within each group, distinctive behaviour, food, reaction to light, etc. (Rakusa-Suszczewski 1972b). Determinations of the dependence of respiration on the dry body weight are also complicated by considerable fluctuations in the lipid content in animals living at sub-zero temperatures. An increase in lipid content is followed by a decrease of the water content. Starvation results in a quicker decrease in lipids in smaller individuals as a result their water content increases. The expression of respiration rate as a function of dry weight causes a decrease of the “ $b$ ” value in the formula  $R = aW^b$ . Relationship between the respiration rate and body weight is based on adaptation at the cellular level including differences in mitochondria, activity of enzymes and the shape of the cells in large and small animals (Prosser

1973). These relationships, however, are not yet fully understood. On the basis of empirical data respiration rate is found to be proportional to body weight raised to the 0.75 power. Divergences from this value are subject of many speculations which result in various proportions suggesting the acceptance of value for "b" other than 0.75 (Winberg 1956, W. Vernberg and I. Vernberg 1972). The exponent "b" is depends on several factors and is not the same for all the various species; it differs in populations separated geographically and depends on the stage of the life cycle, acclimation time and whether standard, routine or active metabolism is measured, (Newell and Northcroft 1967). Data concerning the relationship between oxygen consumption and body weight of invertebrates living normally at sub-zero temperatures are presented in Table I. The exponent "b" values are comparable regardless of the different units in which the remaining parameters of the equation are expressed. As can be seen, the value "b" varies considerably but there is no foundation to suppose that an increase in the respiration rate proportional to the body weight 0.75. does not hold good for organisms at sub-zero temperatures. For statistical analysis, confidence limits must be calculated for both values "a" and "b" which was not always possible to achieve on the basis of the published data given in Table I.

#### 4. Compensation in respiration

Relationship between respiration rate and body weight  $^{0.75}$  give a basis for comparative estimation of respiration of the animals of different body weight adapted to different temperature ranges in their natural habitat. Experimental results concerning temperature dependence of respiration in animals are described by Krogh's (1916) normal curve. Scholander et al. (1953) were among the first to study the respiration of Arctic animals and showed that their respiration was higher than in tropical animals acclimated to low temperatures. The results from those studies served as a basis for interpretation of compensation and description of its different manifestation in ectothermic animals (Prosser 1973). The analysis of respiration-temperature relationships of crustaceans (Suščenja 1972), on the basis of data from the literature, showed that the line interpolating the respiration of different species, especially at low-temperature range, runs higher than the original Krogh's normal curve.

Among studies on respiration of Antarctic *Crustacea* the lowest level was recorded in *Paramoera walkeri* in the winter season (Klekowski, Opaliński and Rakusa-Suszczewski 1973) and approximates the values anticipated from the Suščenja's curve (Fig. 7). The highest level was recorded in *Orchomene plebs* and it is at a level almost equal to the value of oxygen consumption for *Amphipoda* in the resting stage, at the temperature of 20°C. As can be seen from these data the range of oxygen consumption at -1.8°C, in Antarctic species, is very wide. A comparative analysis of the respiration of fish over a wide range of temperatures, including the results from investigation of Antarctic species, was made by Wohlschlag (1963, 1964) (Fig. 8).

Table I

## Relationship between oxygen consumption and body weight of Antarctic invertebrates

Species	T (°C)	Relationship between oxygen consumption and body weight expressed by formula $R = aW^b$	Units	Author
<i>Amphipoda Orchomonella chilensis</i>	-1.8	$b = 0.53^*$	$\mu\text{l O}_2 \cdot \text{h}^{-1} \cdot \text{ind.}^{-1}$	Armitage (1962)
<i>Paramoera walkeri</i>	-1.9	$R = 0.09 W^{0.74 \pm 0.12}$	$\mu\text{l O}_2 \cdot \text{h}^{-1} \cdot \text{ind.}^{-1}$ wet weight	Klekowski, Opaliński and Rakusa-Suszczewski (1973)
<i>Paramoera walkeri</i>	-1.2	$R = 0.27 W^{0.65 \pm 0.14}$	"	Rakusa-Suszczewski and Klekowski (1973)
<i>Orchomene plebs</i>	-1.8	$R = 0.322 W^{0.72 \pm 0.12}$	"	Rakusa-Suszczewski et al. (in prep.)
<i>Orchomene plebs</i>	-1.8	$R = 1.15 W^{0.57 \pm 0.16}$	$\mu\text{l O}_2 \cdot \text{h}^{-1} \cdot \text{ind.}^{-1}$ dry weight	Rakusa-Suszczewski (in prep.)
<i>Orchomene plebs</i>	35 <sup>0/00</sup>			
<i>Orchomene plebs</i>	-1.8	$R = 0.97 W^{0.6 \pm 0.18}$	"	"
<i>Orchomene plebs</i>	23 <sup>0/00</sup>			
<i>Orchomene plebs</i>	-1.8	$R = 0.761 W^{0.66 \pm 0.15}$	"	"
<i>Orchomene plebs</i>	43 <sup>0/00</sup>			
<i>Pycnogonidae</i> 7 species	0.0—1.2	$R = 0.013 W^{0.78 \pm 0.27}$	$\text{mg O}_2 \cdot \text{h}^{-1} \cdot \text{ind.}^{-1}$ wet weight	Calculated from Douglas, Hedgpeth and Hemmingsen (1969)
<i>Astroidea Odontaster validus</i>	-1.8	$R = 0.0253 W^{0.92^*}$	$\text{mg O}_2 \cdot \text{h}^{-1} \cdot \text{ind.}^{-1}$	Dayton et al. (1974)
<i>Odontaster meridionalis</i>	-1.8	$R = 0.0255 W^{0.82}$	$\text{mg O}_2 \cdot \text{h}^{-1} \cdot \text{ind.}^{-1}$ g dry weight	Dayton et al. (1974)
<i>Acodontaster conspicuus</i>	-1.8	$R = 0.0305 W^{0.84}$	"	"
<i>Acodontaster hodgsoni</i>	-1.8	$R = 0.0275 W^{0.81}$	"	"
<i>Perknaster fucus antarcticus</i>	-1.8	$R = 0.0265 W^{0.74}$	"	"
<i>Austrodoris mcmurdensis</i>	-1.8	$R = 0.0860 W^{0.43^*}$	"	"

± conf. limit.

\*) differ from 0.75 significantly

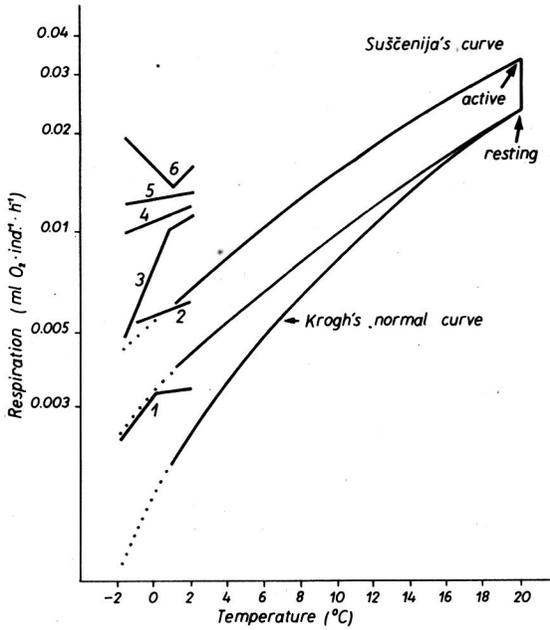


Fig. 7. Compensation in the hypostenothermic *Amphipoda* respiration

The respiration of antarctic species at the sub-zero temperatures is approximate or higher than would be anticipated if the oxygen consumption of *Amphipoda* (0.1 g wet weight) at the temperature of 20° was extrapolated into the sub-zero temperatures zone in accordance with Krogh's normal curve (Winberg 1956) or Suščenija's (1972) curve. 1, 2 — *Paramoera walkeri*, 3, 4, 6 — *Orchomene plebs*, 5 — *Orchomonella chilensis* (full description in Fig. 3.).

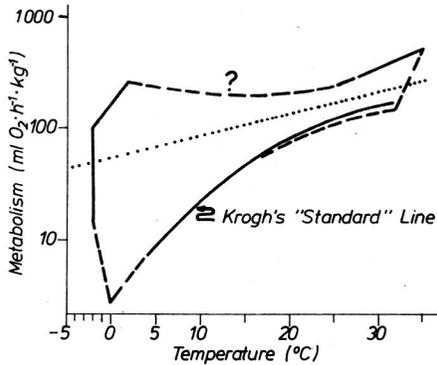


Fig. 8. Schematic of metabolism-temperature relation-ships of fishes adapted to various environments (Wohlschlag 1964 with modifications)

Similarity to metabolism-temperature relationship of *Crustacea* (*Amphipoda*) is visible.

Oxygen consumption of endemic species of the genus *Trematomus* is much higher than could anticipated from the normal curve extrapolated into sub-zero temperature range. However, in fish of *Rhigophila* genus respiration rates were approximate to values anticipated from the normal curve at

a temperature of  $-2.0^{\circ}\text{C}$ . Everson and Ralph (1970) investigated respiration of white-blooded Antarctic fish of *Chaenocephalus* genus at temperatures between  $0.4$  and  $1.5^{\circ}\text{C}$ . The values of oxygen consumption were lower than in fish of *Trematomus* genus by Wohlschlag. Holeyton (1974) calls into question the results of respiratory measurements published by Wohlschlag (1963, 1964) considering the values to be over-estimated due to study of individuals in a state of abnormal activity. Regardless of the final result of the controversy over the existence and scope of compensation, the wide range of oxygen consumption in organisms living under sub-zero temperatures is real (Figs. 7 and 8).

The term compensation covers various compensatory mechanisms comprising selective synthesis of protein isoenzymes, lowering of the energy of activation of enzymes, changes in lipid etc. and it is still not clear which of them play a decisive role (cf. Newell 1973). In our point of view, therefore, compensation in respiration is not a necessity but a potential possibility for providing a higher metabolic rate of organisms living under sub-zero temperatures, as compared with organisms living in natural environment at above-zero temperature which varies considerably.

## 5. References

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