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Russian/German Cooperation at the White Sea: Physiological Adaptations of Marine Invertebrates to a Life at Different Climatic Zones

Kurzfassung

Der Artikel stellt Ergebnisse aus einer Zusammenarbeit zwischen der Stiftung Alfred-Wegener-Institut, Bremerhaven, und dem Zoologischen Institut, St. Petersburg, dar. Es wurden Stoffwechseluntersuchungen an Pierwürmern (*Arenicola marina*, Polychaeta) aus subpolaren und gemäßigten Klimazonen zu verschiedenen Jahreszeiten durchgeführt, um die Mechanismen zu studieren, die eine Anpassung an ein Leben in verschiedenen Klimazonen erlauben und die einer Anpassung Grenzen setzen.

Abstract

The article presents results from a co-operation between the Alfred Wegener Institute, Bremerhaven, and the Zoological Institute of St. Petersburg. The physiological adaptations of lugworms (*Arenicola marina*, Polychaeta) collected from subpolar and boreal habitats and at different seasons (summer or winter) were examined to study possible adaptations or limitations of a life in different climatic zones.

Résumé

L'article présente des résultats obtenus par la coopération entre l'Institut Alfred Wegener à Bremerhaven et l'institut zoologique à St. Pétersbourg. On a fait, durant diverses saisons, des analyses de métabolisme concernant des vers, *Arenicola marina*, provenant de zones climatiques bien différentes, pour étudier les mécanismes qui permettent ou qui limitent une adaptation à la vie dans diverses zones climatiques.

Keywords

Arenicola marina, Cold Adaptation, Critical Temperature, Mitochondria

1. Introduction

Ectothermal animals are directly influenced by temperature since the rates of biochemical and physiological processes change and extreme temperatures or temperature variations can cause lethal injuries. Recently, the effects of temperature on marine coastal ecosystems have come into focus owing to the process of global warming and an observed shift in the geographical distribution of various marine animals. We tried to identify physiological constraints determining and limiting thermal adaptations and specialisations, to assess the impact of environmental temperatures and their change on the geographical distribution of animals (PÖRTNER 2001). Field studies were performed during annual expeditions into the polar or subpolar regions. Summer laboratories were set up close to the areas where the animals came from, to avoid distortion of the data by transportation or maintenance stress. A cooperation between the Alfred Wegener Institute for Polar and Marine Research in Bremerhaven and the Zoological Institute of St. Petersburg of the Russian Academy of Sciences opened the possibility to conduct field and laboratory studies at the subpolar White Sea (Fig. 1). Results of this cooperation were presented at this symposium.

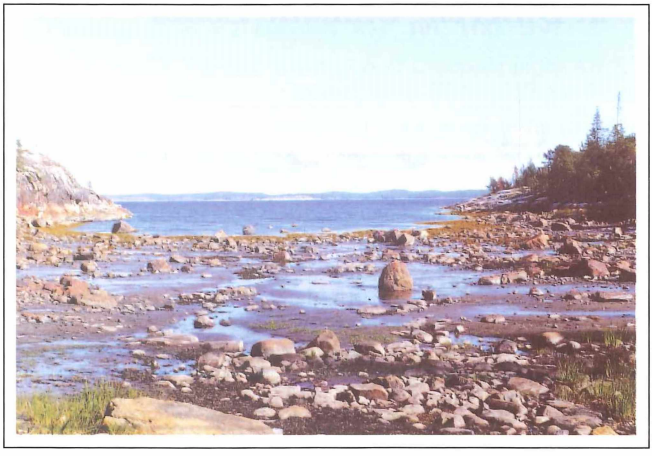


Fig. 1: The White Sea Biological Station, the field station of the Zoological Institute of St. Petersburg in Russia, is situated at the end of the largest estuary in the Kandalaksha Bay, the Chupa estuary, close to the Arctic cycle. In neighbouring small inlets intertidal communities can be studied.



Fig. 2: The polychaete lugworm *Arenicola marina* can be found in coastal areas of nearly the whole northern hemisphere. There it is exposed to different climates and to seasonal and diurnal temperature changes. Therefore, this worm is a suitable model to study temperature adaptation in marine invertebrates.

2. Observations and Results

In different marine invertebrates, like in the intertidal lugworm *Arenicola marina* (Polychaeta) (Fig. 2), low and high critical temperatures (Tc) could be identified, that are characterized by the onset of anaerobic metabolism (Fig. 3, SOMMER et al. 1997). The general conclusion from this work and from comparative analysis in several marine invertebrate and fish species is that, at extreme temperatures the capacity of ventilation and circulation is insufficient to supply cells with enough oxygen to meet their energetic demand – even under normoxic conditions (for review see PÖRTNER 2001). Additional anaerobic energy production is required. However, use of anaerobic metabolism is more of an emergency solution and thus works less efficiently than aerobic energy production. An energy deficiency may occur if the unfavourable conditions prevail for too long.

Acclimation to changing temperatures is supported in marine invertebrates and fishes by changes in the intracellular acid-base milieu. Acid-base regulation is based on passive and active ion regulation and is energetically costly (PÖRTNER et al. 2000). It was found that the intracellular pH (pH_i) in the body wall musculature of *A. marina* decreased linearly with rising temperature in accordance with the alphastat hypothesis, but only within the thermal tolerance range (SOMMER et al. 1997). The alphastat hypothesis says, that the pH value is regulated in such a way, that the protonation of special residues in enzymes (histidine residues) will be kept constant (REEVES 1972). This is necessary to keep enzyme activity constant in spite of temperature changes. However, beyond the critical thresholds the pH_i/temperature relationship was no longer linear. The deviation from linearity was caused by metabolic acidification and, possibly, by a failure of the cells to activate pH_i adjustment due to a lack of energy.

Latitudinal or seasonal temperature adaptation that led to a shift of both critical temperature thresholds could be explained by reduction of the energy consumption in the warm or alternatively improvement of energy production in the cold, so that the initial transition to anaerobic metabolism is reversed. Mitochondria are the cell organelles that are responsible for aerobic energy production. The temperature dependence of mitochondrial functions and mitochondrial densities were investigated in cold adapted lugworms from the White Sea (subpolar summer) and cold (winter) or warm (summer) acclimatised lugworms from the North Sea (boreal), to identify potential mechanisms of energetical adjustment to the environmental temperature regime.

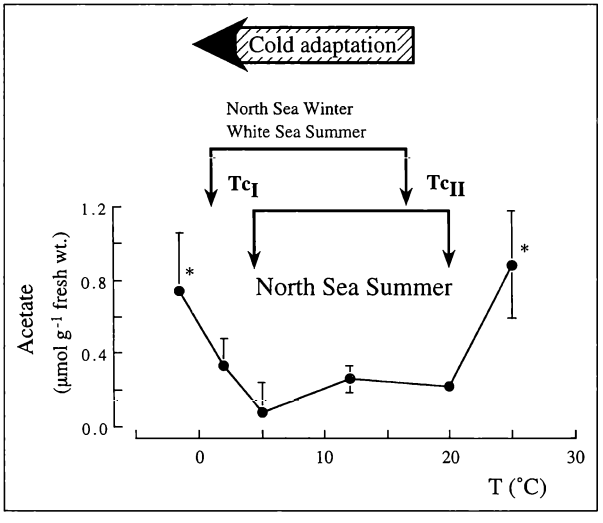


Fig. 3: A low (Tc_I) and a high (Tc_{II}) critical temperature could be characterized in the polychaete lugworm *A. marina* by the accumulation of anaerobic endproducts, like the volatile fatty acid acetate, in the body wall tissue. Subpolar and seasonally cold acclimatised worms displayed lower Tc values than boreal summer animals (mean ± S.D.; n = 5; * = significantly different from the control value at 12°C; modified after SOMMER et al. 1997).

Adaptation to lower mean annual temperatures in White Sea animals was reflected by a 2.4 times higher mitochondrial volume density in the muscle tissue of subpolar compared to boreal specimens. A higher mitochondrial density increases aerobic capacity at low temperatures. It may also compensate for a reduced diffusibility of metabolites and enzymatic substrates that restrict substrate turnover and energy production at low temperatures. This results in a downward shift of the low critical temperature, beyond which anaerobic metabolism sets in. In addition to a higher number of mitochondria per cell, mitochondrial activity was increased in White Sea worms compared with North Sea animals. Mitochondria from White Sea lugworms were characterized by a 2.7 times higher substrate oxidation rate (nmol $O \cdot min^{-1} \cdot mg^{-1}$ mitochondrial protein) in state 3 respiration, i.e. while performing oxidative phosphorylation. Activities (units $\cdot g^{-1}$ fresh wt.) of the mitochondrial enzymes cytochrome c-oxidase (CYTOX) and NADP dependent isocitrate dehydrogenase (IDH) were also higher in subpolar compared with boreal animals. Higher activities may partly result from an increased expression of enzymes within each mitochondrion. However, values of activation energy (Ea) for mitochondrial state 3 respiration at low temperatures and for the oxidation of cytochrome c were found to be reduced in the subpolar worms. This results in a higher activity in spite of low temperatures and in this way may compensate for a lower thermal energy available in the environment of the White Sea animals.

Distinct catalytic properties of enzymes can be achieved by the expression of different isozymes. An electrophoretic analysis of the genetic constitution of *A. marina* revealed significantly different allele frequencies of the enzymes glucose phosphate isomerase and phosphoglucomutase in the White Sea population compared with different European Atlantic populations (from France, the Netherlands, Germany and Norway, HUMMEL et al. 1997). This is indicative of reduced gene flow, probably due to the geographical and hydrographical isolation of the White Sea. The expression of mitochondrial isocitrate dehydrogenase 2 (IDH2) seemed to be majorly determined by temperature in all populations, deduced from the very strong correlation between the allele frequencies of IDH2-A and IDH2-B and the average water temperature (Fig. 4). These findings support the hypothesis, that mitochondria play a key role in the adaptation of marine ectotherms to different temperature regimes.

As a drawback, a higher mitochondrial density and enzyme activities lead to a higher oxygen demand due to the rise in mitochondrial maintenance costs (e.g. for proton and ion gradients and protein synthesis, PÖRTNER et al. 1998). This results in a rise of the whole animal standard metabolic rate and shifts the high Tc to lower temperatures. An increase in the Ea value for the decarboxylation of isocitrate and a lower activity of citrate synthase (CS) in White Sea specimens may help to minimize the increment in standard metabolic rate induced by the higher mitochondrial density and capacity, at the expense of a higher thermal sensitivity of metabolism in the warm.

In contrast to cold adaptation in a latitudinal cline, seasonal acclimatisation to winter conditions in North Sea lugworms seems to consist in a drop in energy demand instead of a rise in energy production. The content of extractable mitochondrial protein in the body wall tissue of North Sea lugworms fell in parallel to a decrease in the acclimation temperature. A lower protein content indicates lower mitochondrial density. This diminishes the oxygen demand of whole animals required to maintain mitochondrial functions. However, it also decreases aerobic capacity. Winter animals compensated this by increasing the capacity of each individual mitochondrion, reflected by elevated rates of state 3 respiration (Fig. 5) and CS activity with decreasing acclimation temperatures. Phosphorylation efficiency and mitochondrial coupling were also higher in winter than in summer specimens (both from the North and the White Seas). State 4 respiration in the presence of oligomycin (state 4ol), an inhibitor of mitochondrial F_0F_1-ATPase, vastly quantifies the proton leakage rates through the inner mitochondrial membrane. No difference in proton leakage rates were observed between cold adapted

White Sea lugworms and cold acclimatised winter animals from the North Sea. However, state 4ol respiration rates in summer animals from the North Sea were significantly reduced. Nevertheless, the percentage of oxygen needed to fuel the proton leak during state 3 respiration was lowest in winter animals compared to summer animals from the North or White Seas due to elevated state 3 respiration rates in winter lugworms (Fig. 5, SOMMER & PÖRTNER, unpublished).

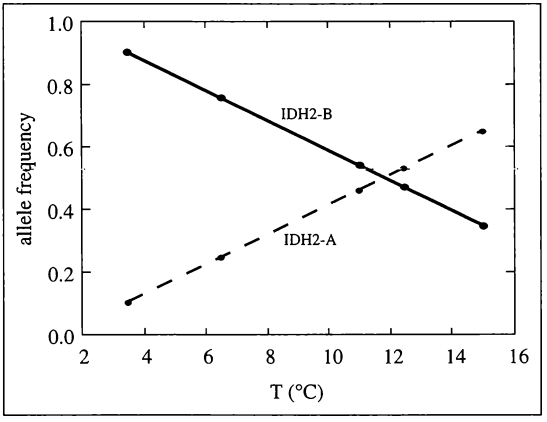


Fig. 4: A strong correlation exist between the allele frequencies of mitochondrial isocitrate dehydrogenase 2 (IDH2–A and IDH2–B) and the average water temperature at the sampling location. The expression of IDH2, therefore, seems to be predominantly determined by temperature in all studied populations (in the White Sea population as well as in Atlantic populations from France, the Netherlands, Germany and Norway; modified after HUMMEL et al. 1997)

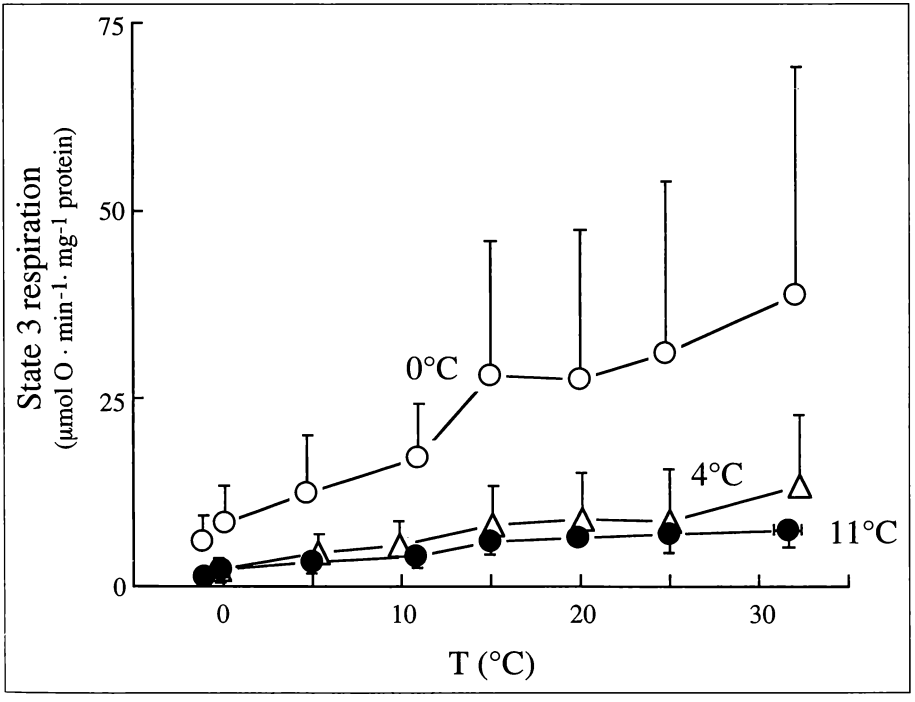


Fig. 5: Seasonal cold acclimatisation in North Sea lugworms is associated with a rising capacity of mitochondrial succinate oxidation. Mitochondria of 0°C acclimated lugworms had a significantly higher oxygen consumption rate in state 3 than mitochondria from 4 or 11°C acclimated worms (mean ± S.D.; n = 6–8)

3. Conclusion

In conclusion, physiological adaptation to different temperatures in marine ectothermal animals is linked to energy metabolism. Beyond critical temperature thresholds, insufficient ventilation or circulation limit aerobic energy production. Anaerobic metabolism sets in. Cold adaptation or acclimatisation in the lugworm *A. marina* led to decreasing low critical temperatures. Latitudinal cold adaptation of White Sea lugworms led to an increased aerobic capacity, so that the animals may stay active in spite of prevailing lower mean annual temperatures, but at the expense of a higher basal metabolic rate. In contrast, it seems that a rising efficiency of aerobic energy production in boreal winter animals is associated with metabolic depression at the expense of decreased proton leak during state 3 respiration and, therewith, decreased regulatory flexibility.

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