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ORIGINAL PAPER

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Distribution patterns of decapod crustaceans in polar areas: a result of magnesium regulation?

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Abstract Nearly all decapod crustaceans found in Antarctic waters south of the Antarctic Convergence are caridean shrimps (Natantia) while the group of Reptantia is largely absent in this area. Progress in the development of a physiological hypothesis is reported, which explains this distribution pattern based on differences in the regulation of magnesium levels in the haemolymph ($[Mg^{2+}]_{HL}$) and on the Mg^{2+} dependence of threshold temperatures below which cold-induced failure of cardiac and ventilatory performance occurs. Previous studies had shown that an increase in oxygen consumption and activity levels in the cold can be induced by experimental reduction of $[Mg^{2+}]_{HL}$ in different reptant decapod species. In the present study, we tested the potential of these experimental findings for predicting the effect of low $[Mg^{2+}]_{HL}$ in nature, and investigated temperature-induced changes in oxygen consumption in two species with low but different $[Mg^{2+}]_{HL}$ from southern Chile, *Halicarcinus planatus* and *Acanthocyclus albatrossis* ($[Mg^{2+}]_{HL} = 10.7$ and 21.6 mmol l^{-1}, respectively). In accordance with previous findings, low $[Mg^{2+}]_{HL}$ levels were associated with a reduction of thermal sensitivity and a higher metabolic rate in the cold. A model is developed which describes how $[Mg^{2+}]_{HL}$ reduction caused a threshold temperature (pejus temperature, Tp) to fall, which characterises the onset of cold-induced failure in oxygen supply to tissues. This threshold temperature is interpreted, not only to indicate the limits of cold tolerance, but also of geographical distribution. Tp is shifted towards lower temperatures in Natantia, which are efficient $[Mg^{2+}]_{HL}$ regulators. In contrast, Reptantia, which are poor $[Mg^{2+}]_{HL}$ regulators, appear unable to colonise the permanently cold water of the Antarctic due to insufficient capacity of cardiac performance and, therefore, largely reduced scope for activity at high $[Mg^{2+}]_{HL}$.

Introduction

Early investigations of the Antarctic shelf fauna seemed to indicate that decapod crustaceans are very rare south of the Antarctic Convergence (Yaldwyn 1965). However, more recent studies, especially in the Weddell Sea, revealed a well-established decapod fauna with eight different species out of seven families (Arntz and Gorny 1991; Arntz et al. 1994), which all belong to the group Caridea (Natantia). The group of Reptantia, which is otherwise very successful in colonising different and even extreme habitats, is almost completely absent in the high Antarctic. Different hypotheses were developed to explain the absence of this whole group of crustaceans, mainly based on larval, ecological or geohistorical patterns. Nevertheless, none of these hypotheses provides a commonly accepted explanation (reviewed by Arntz et al. 1994). This paper reports recent progress in the development of a physiological hypothesis, which explains the absence of Reptantia in the Antarctic based on their inability to regulate magnesium in the haemolymph ($[Mg^{2+}]_{HL}$) at low levels, thereby exacerbating problems of oxygen supply to tissues due to limitations of cardiac and ventilatory performance at low temperatures (Frederich et al. 2000a).

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Results and discussion

Crustacean haemolymph is usually more or less isoionic to seawater except for Mg^{2+} (Robertson 1960; Mantel and Farmer 1983). Mean $[Mg^{2+}]_{HL}$ of caridean shrimps is found at 5–12 mmol l^{-1}, far below the magnesium concentration of seawater (53 mmol l^{-1}). In contrast, most Reptantia regulate $[Mg^{2+}]_{HL}$ at levels between 30 and 50 mmol l^{-1}, close to seawater concentrations (Walters and Uglow 1981; Tentori and Lockwood 1990). This difference is of special interest since there is a close relationship between $[Mg^{2+}]_{HL}$ and activity. In crustaceans, low $[Mg^{2+}]_{HL}$ values are clearly correlated with higher activity levels, while high $[Mg^{2+}]_{HL}$ values are usually combined with lower activity levels. This holds true for comparisons of activity levels between different species, as well as for comparisons between long-term periods with different levels of activity, like hibernation, within the same species (Robertson 1953, 1960; Kayser 1961; Walters and Uglow 1981; Morritt and Spicer 1993; Spicer et al. 1994). This correlation between $[Mg^{2+}]_{HL}$ and activity has been known for a long time. Pantin (1946) suggested a formula with high $[Mg^{2+}]$ to anaesthetise invertebrates, and Robertson (1953) described species such as *Maja squinado* with their high $[Mg^{2+}]_{HL}$ as "living in a semi-narcotized state".

Elevated activity levels require an adequate oxygen supply to tissues by ventilation and circulation. Several studies have shown that oxygen may become a limiting factor at extreme temperatures and, consequently, both low and high threshold temperatures were defined by the onset of anaerobic metabolism in both invertebrates and fish (Zielinski and Pörtner 1996; Sommer et al. 1997; Pörtner et al. 1998, 2000; Sommer and Pörtner 1999; van Dijk et al. 1999 ; Frederich and Pörtner, 2000). Cold adaptation elicits a shift of both threshold temperatures to lower values to enable the animals to remain fully active at low temperatures.

In previous experimental studies of the effects of temperature and various $[Mg^{2+}]_{HL}$ levels on the physiology of reptant decapod crustaceans, $[Mg^{2+}]_{HL}$ was reduced from 45 to 8 mmol l^{-1} by exposing specimens of *M. squinado*, *Hyas araneus* and *Eurypodius latreillei* to seawater with artificially reduced $[Mg^{2+}]$ of approximately 6 mmol l^{-1} (compared to 53 mmol l^{-1} in natural seawater). Animals were subsequently incubated at different temperatures and motor activity, heart rate, oxygen consumption or oxygen tensions in the haemolymph were investigated. As described in detail elsewhere (Frederich et al. 2000a), heart rate of control animals in *H. araneus* ($[Mg^{2+}]_{HL}$ 46 mmol l^{-1}) decreased linearly between 7.2 and –1.2°C by 72.7 ± 13.0%. Heart rate in $[Mg^{2+}]_{HL}$-reduced animals ($[Mg^{2+}]_{HL}$ 8 mmol l^{-1}) decreased significantly less – by only 37.2 ± 17.5%. A different pattern was visible in *E. latreillei*. Heart rate and oxygen consumption decreased linearly in control animals ($[Mg^{2+}]_{HL}$ 45 mmol l^{-1}) and in $[Mg^{2+}]_{HL}$-reduced animals ($[Mg^{2+}]_{HL}$ 8 mmol l^{-1}). Nevertheless, both parameters were found at significantly elevated levels at all temperatures in $[Mg^{2+}]_{HL}$-reduced animals.

The availability of oxygen to tissues depends upon oxygen uptake by ventilation and on oxygen distribution via haemolymph circulation (cardiac output). These two parameters showed a strong temperature dependence in *M. squinado* (as described in detail in Frederich et al., 2000b). Cardiac output decreased linearly during progressive cooling between 12 and 8°C. An overproportional drop led to very low values between 7 and 0°C. This overproportional drop was also visible in ventilation and occurred between 7 and 6°C, followed by a transient increase around 4°C. Arterial PO_2 remained almost constant between 12 and 8°C and decreased slightly between 8 and 6°C in accordance with reduced cardiac and ventilatory activities. The lowest PO_2 values were reached below 1°C when ventilation had stopped. The overproportional drop in ventilation and circulation could be shifted to lower temperatures when reducing the $[Mg^{2+}]_{HL}$ from 39.9 ± 4.6 to 6.1 ± 0.7 mmol l^{-1}. These previous findings are summarised schematically in Fig. 1, which demonstrates the two patterns of shifting performance of different parameters due to the reduction in $[Mg^{2+}]_{HL}$.

After these initial findings, the question remained open as to whether an experimental reduction of $[Mg^{2+}]_{HL}$ has any relevance for being able to predict the ability of reptant decapods to survive in cold ocean environments. We therefore chose to compare two decapod crustacean species with different, but relatively low, $[Mg^{2+}]_{HL}$, the two South American intertidal crabs *Halicarcinus planatus* and *Acanthocyclus albatrossis*. Both species display lower $[Mg^{2+}]_{HL}$ than most other brachyurans: 21.6 mmol l^{-1} in *A. albatrossis* and only 10.7 mmol l^{-1} in *Halicarcinus planatus*. Both species live

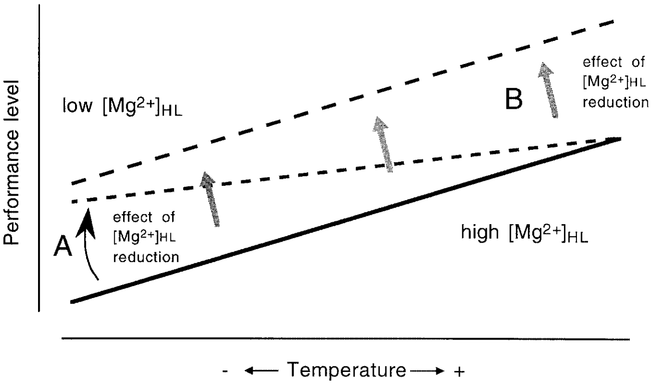

Fig. 1 Schematic presentation of a shift in performance parameters crucial for survival (motor activity, heart rate, oxygen consumption) which is induced by lowering $[Mg^{2+}]_{HL}$ experimentally in various reptant decapod species, evidenced by analyses in *Hyas araneus*, *Maja squinado* and *Eurypodius latreillei*. Lowering $[Mg^{2+}]_{HL}$ in *E. latreillei* resulted in a parallel upward shift (*B*) while in other investigated species the effect of reduced $[Mg^{2+}]_{HL}$ was visible only at lower temperatures (*A*). The reason for this difference remains unclear (based on data by Frederich et al. 2000, 2000a)

in the same environment and inhabit a comparable ecological niche. The reasons for the different capacities of $[Mg^{2+}]_{HL}$ regulation remain obscure since no data are available on the autecology of the two species. In accordance with findings obtained in *M. squinado* at experimentally reduced $[Mg^{2+}]_{HL}$, thermal sensitivity of oxygen consumption in the cold differed between the two species, reflected by different Q_{10} values (Fig. 2). In *A. albatrossis*, the species with higher $[Mg^{2+}]_{HL}$, oxygen consumption decreased, with a Q_{10} of 6.8 between 8.8 and –1°C, while the Q_{10} of 1.3 in *Halicarcinus planatus* was significantly lower in the same temperature range ($n = 5$ per species and group, ANCOVA, $P < 0.05$). In support of the patterns depicted in Fig. 1, oxygen consumption of the species with the lower $[Mg^{2+}]_{HL}$, *Halicarcinus planatus*, was threefold higher at subzero temperatures than in *A. albatrossis*.

As summarised in Fig. 1, an elevation of activity can be elicited by a reduction of $[Mg^{2+}]_{HL}$ especially at cold temperatures. Owing to the reduction of thermal sensitivity, $[Mg^{2+}]_{HL}$-reduced crabs displayed elevated heart rates and oxygen consumption values and reacted faster to experimental stimulation, regardless of whether $[Mg^{2+}]_{HL}$ was reduced experimentally or in nature (Fig. 2). Animals were able to survive experimental reductions of $[Mg^{2+}]_{HL}$ for several months, which indicates that elevated $[Mg^{2+}]_{HL}$ levels are not essential for survival, at least under laboratory conditions.

The first report of an effect of experimental $[Mg^{2+}]_{HL}$ reduction on crustaceans is given by Holliday (1980), who described *Cancer magister* held in Mg^{2+}-free seawater as being "easily excited and aggressive". This corresponds to the results reported in this paper. Elevated excitability and activity might be explained by the inhibitory effect of Mg^{2+} on synaptic transmitter release at the nerve-muscular junction, and by the competitive inhibition of calcium binding (Katz 1936; Del Castillo and Katz 1954; Wernig 1972; Dudel et al. 1982; Howarth and Levi 1998). In accordance with the findings already outlined, elevated levels of Mg^{2+} seem to act more as a relaxant than as an anaesthetic (Sartoris and Pörtner 1997; Frederich et al. 2000a).

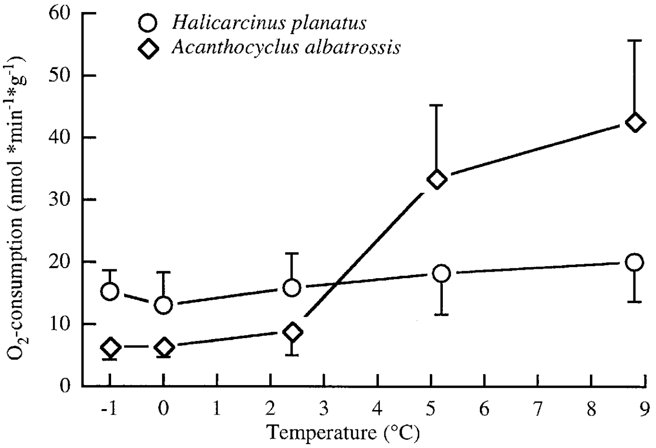

Fig. 2 Oxygen consumption of *Halicarcinus planatus* and *Acanthocyclus albatrossis* at different temperatures. Thermal sensitivity was found to be significantly lower in *H. planatus* at $[Mg^{2+}]_{HL} = 10.7$ mmol l^{-1} compared to *A. albatrossis* at $[Mg^{2+}]_{HL} = 21.6$ mmol l^{-1} ($n = 5$ per species and group, ANCOVA, $P < 0.05$)

The question of why Reptantia regulate $[Mg^{2+}]_{HL}$ to higher levels compared to Natantia is still open. Few studies indicate that there might be differences in the mechanisms of $[Mg^{2+}]_{HL}$ regulation between Caridea and Brachyura (Holliday 1980; Franklin et al. 1987) but further investigations are necessary to elucidate the details.

The anaesthetising effect of Mg^{2+} in the cold becomes important in the context of the concept that oxygen is an important factor for defining threshold values at extreme temperatures. At both low and high critical temperatures, animal metabolism switches from aerobiosis to anaerobiosis, and anaerobic endproducts accumulate (reviewed by Pörtner et al. 1998, 2000). In these studies the ambient oxygen did not become limiting, but oxygen supply to tissues did. Therefore, ventilatory and cardiac performance may play an important role in defining thermal tolerance. As shown previously, arterial haemolymph PO_2, which represents the pressure head for oxygen diffusion into tissues, is correlated with heart and ventilation rates (Frederich and Pörtner, 2000). The oxygen-binding properties of haemocyanin may change with temperature also; however, since the haemocyanin acts as an oxygen buffer to support maintenance of body fluid PO_2, analysis of PO_2 gives the most relevant information on the quality of tissue oxygenation.

The findings of decreasing levels of haemolymph PO_2 and thus progressive oxygen limitation towards high and low temperature extremes led us (Frederich and Pörtner, 2000) to develop a model in accordance with the "law of tolerance" (Shelford 1913, 1931, Fig. 3). The limiting parameter, arterial PO_2, and the progressive failure of cardiac and ventilatory performance towards extreme temperatures characterise various sections of the tolerance range (Fig. 3A). Within the optimum range, oxygen availability and, in consequence, scope for aerobic activity is maximal. The onset of a decrease in arterial haemolymph PO_2 at pejus temperatures (Tp; Frederich and Pörtner, 2000; pejus = getting worse) reflects reduced aerobic scope for activity and is accompanied by progressively insufficient cardiac and ventilatory performance. Transitions from pejus to pessimum ranges at critical temperatures (Tc, Pörtner et al. 1998, 2000) are characterised by the onset of anaerobic metabolism and, in consequence, the accumulation of anaerobic endproducts. Within pessimum ranges, survival becomes a question of time due to insufficient oxygen availability. The upper and lower Tc encompass the range of physiological tolerance.

For *M. squinado*, upper and lower Tp values agree well with the annual minimum and maximum mean temperatures of the environment in the investigated

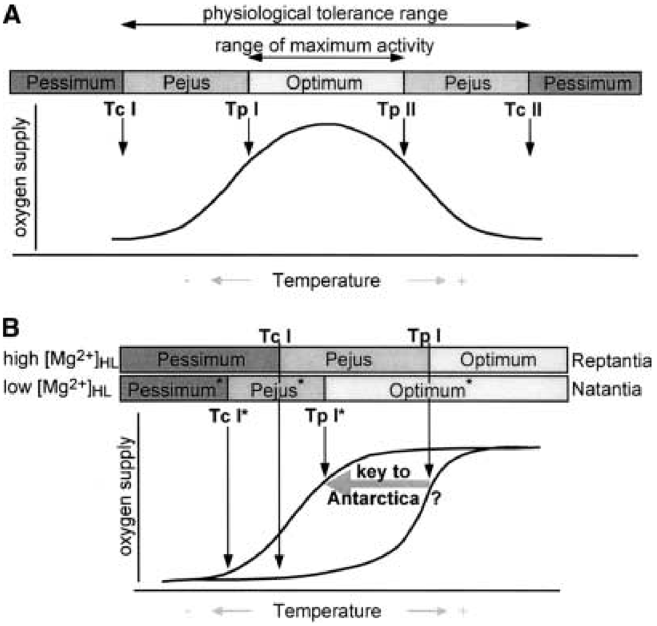

Fig. 3A, B Diagram of physiological threshold temperatures inserted into the law of tolerance. **A** Pejus temperatures (*Tp*) and critical temperatures (*Tc*) are set by the availability of oxygen to tissues and, therefore, depend on ventilatory and circulatory performance (modified after Frederich and Pörtner, 2000). **B** The higher efficiency of $[Mg^{2+}]_{HL}$ regulation in Natantia shifts both pejus and critical threshold values to lower temperatures compared to Reptantia with less effective $[Mg^{2+}]_{HL}$ regulation. This shift is most likely a crucial preadaptation for surviving colder temperatures and, therefore, the physiological key for the colonisation of Antarctic shelves by crustaceans

population (Dauvin et al. 1991; Sournia and Birrien 1995) and, therefore, it can be inferred that the Tp values may limit the ecological tolerance range. In this ecological tolerance range, full scope for activity is available to the animals. In consequence, cold adaptation requires an adaptational shift of both Tp and Tc values towards lower temperatures to maintain sufficient aerobic activity. This likely involves an adjustment of mitochondrial density and capacity (Pörtner et al. 1998, 2000). As a further step forward in the development of the model depicted in Fig. 3A, it appears that high $[Mg^{2+}]_{HL}$ prevents the shift of Tp and Tc to subzero temperatures and thereby limits the capacity of cold adaptation (Fig. 3B).

In summary, the present study shows that slow-moving and sluggish species of Reptantia can be triggered to become more active by decreasing $[Mg^{2+}]_{HL}$ to levels comparable to those found in caridean shrimps. Survival in the natural environment requires sufficient aerobic scope for escape, predation or reproduction. While cold temperatures minimise activity, low $[Mg^{2+}]_{HL}$ levels shift the pejus temperature and, accordingly, the optimum range towards lower values (Fig. 3B). A concomitant shift of the critical temperature is likely. Small differences in cold tolerance by just 1 or 2°C result (Fig. 3) and lead to an exclusion of Reptantia from areas with extremely low temperatures in both the Arctic and the Antarctic, where they are only found at temperatures close to 0°C and above (Frederich et al. 2000).

It appears likely that efficient $[Mg^{2+}]_{HL}$ regulation in Natantia was an important preadaptation for surviving the cooling of Antarctica during the Tertiary (Clarke and Crame 1989; Clarke 1990) or allowed successful recolonisation after glaciation cycles (Brey et al. 1996). In contrast, Reptantia with less efficient $[Mg^{2+}]_{HL}$ regulation are narcotised by the combination of low temperatures and high $[Mg^{2+}]_{HL}$ and, in consequence, may have been unable to remain in the Antarctic or to recolonise the shelves after glaciation. Nonetheless, the ability to maintain sufficient levels of motor activity in the cold is obviously only one precondition for survival in the Antarctic environment, which needs to be complemented by adequate lifestyle adaptations.

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