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Comparative studies on the metabolic rate of the isopod *Idotea chelipes* (Pallas) inhabiting different regions of the Baltic Sea

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Abstract

The heat production rate of the euryhaline isopod *Idotea chelipes* inhabiting two geographically and ecologically different regions, the Gulf of Gdansk (6.8 psu) (psu, practical salinity unit) and the Mecklenburg Bay (11.8 psu), was examined by direct calorimetry. The wet weights of specimens from the two regions varied from 0.005 to 0.030 g and between 0.004 and 0.036 g for *I. chelipes* from the Gulf of Gdansk and Mecklenburg Bay, respectively, and were not statistically different ($P > 0.05$). Animals that exhibited locomotor activity were characterized by metabolic rates higher by 12–77% compared to those of inactive specimens. The mean specific metabolic rates of *I. chelipes* from the Gulf of Gdansk and Mecklenburg Bay were 7.5 ± 3.4 J h^{-1} g^{-1} ww ($n = 28$) and 8.4 ± 2.6 J h^{-1} g^{-1} ww ($n = 28$), respectively. Metabolic rates of males and females were not significantly different ($P > 0.05$). The statistically significant ($P < 0.05$) relationship between specific metabolic rate (SMR) and wet weight (ww) was described within the experimental mass range by the power functions $SMR_1 = 0.53ww_1^{-0.56}$ ($R = -0.48$) for *I. chelipes* from the Gulf of Gdansk and $SMR_2 = 0.32ww_2^{-0.75}$ ($R = -0.63$) for those from Mecklenburg Bay.

Keywords: *Idotea chelipes*; Baltic Sea; Direct calorimetry; Metabolic rate

1. Introduction

Rate and efficiency of metabolic processes in animals are affected by various factors, including intrinsic ones like size, sex or locomotor activity as well as environmental ones like temperature, salinity or dissolved oxygen [1]. Two populations of the same species inhabiting geographically and ecologically different environments can exhibit altered metabolic responses to changing factors [2]. This might be due to the genetic differences created during species speciation [3]. The metabolic response to any of the environmental factors might also result from the characteristic specificity of the species [4].

Measurements of metabolic rates provide information on the energy status of organisms and are regarded as an important element in studies of energy flow in marine organisms and populations [5]. They are also useful tools in comparative studies of animal adaptation and performance [6]. The most accurate method of metabolic measurement is to determine how much heat is produced by an organism [7]. This is the sum of all exothermic and endothermic processes, and it allows for the determination of both aerobic and anaerobic metabolism [8,9].

Idotea chelipes is a widely ranging benthic crustacean in European coastal waters. This species is of brackish water origin and occurs in different types of aquatic biotopes ranging from the brackish waters of estuaries (4–6 psu) to marine waters (32–39 psu) [10,11]. *I. chelipes* inhabits the phytal of coastal lagoons where it is a common component of the ben-

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thic fauna. It is a herbivore and itself a food item for many fish species [12].

The aim of the current study was to determine the metabolic rate of *I. chelipes* and the effect of size and sex using direct calorimetry. Whether or not there are differences in metabolic rates between two populations from different regions of the Baltic Sea – the Gulf of Gdansk (Poland, 6.8 psu) and Mecklenburg Bay (Germany, 11.8 psu) – was also investigated.

2. Material and methods

I. chelipes specimens were collected in August 2003 in the coastal zones of the Gulf of Gdansk ($S = 6.8$ psu; $T = 18\,^{\circ}C$) and Mecklenburg Bay ($S = 11.8$ psu; $T = 18\,^{\circ}C$). Macroalgae of the genus *Enteromorpha* and *Cladophora*, which were used as feed for the isopods, were sampled at the same time. The amphipods were held in the laboratory for 7 days at the temperature and salinity of their natural habitat. The total metabolic rate was determined based on heat production measurements conducted in an isothermal LKB 10700-2 batch calorimeter (Bromma, Sweden) described by Bengtsson [13] and modified by Linke [14,15]. Before and after the measurements, the base line (the calorimetric signal without animals) was determined. Single animals were transferred to a vessel containing 3 ml of filtered (cellulose filter, 0.45 μm), well-oxygenated water at the appropriate salinity and at a temperature of 18 °C. Heat production measurements were conducted during 90 min after an equilibration time of about 60 min. The oxygen tension of the medium, measured with a needle microelectrode (PA 2000, Unisense, Denmark), dropped by about 30% during the experiment period. At the end of the experiment, the length from the head to the end of the telson and the sex [16] of the specimens were determined. Surface water was blotted off the animals with soft tissue paper and sample wet weight was determined to the nearest milligram. The specimens were dried at 55 °C for 48 h and weighed again.

The specific metabolic rate (SMR) of a single animal expressed in Joules per hour per gram wet weight ($J\,h^{-1}\,g^{-1}$ ww) was calculated with the following equation (1):

$$\mathrm{SMR} = \frac{Uk}{m} \quad (1)$$

where U is the mean calorimetric signal (μV) corresponding to the heat production (level without activity peaks) for the studied time period (μV), k the calorimeter sensitivity $1.43\,10^{-5}\,W\,\mu V^{-1}$ and m is the wet weight of the studied organism (g).

All values are presented as the mean with standard deviation (mean ± S.D.). Power regressions ($y = ax^b$), and correlation coefficients (R) were used to describe the relationship between the investigated parameters. The significance of the obtained differences was tested with the Mann–Whitney U-test at a significance level of 5%.

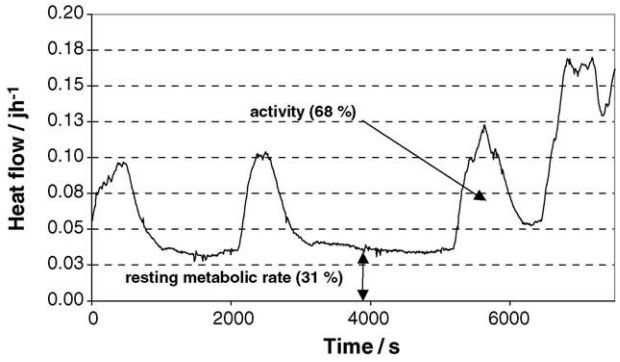

Fig. 1. Example of power–time curves of *I. chelipes* males from the Gulf of Gdansk with periods of resting and active metabolism rate.

3. Results

I. chelipes exhibited different levels of activity during the measurements (Fig. 1). Based on the analyses of the power–time curves, it was determined that the energetic cost of locomotor activity of this species from the Gulf of Gdansk was an average of 43% (12–77%) of the total metabolic rate. In animals from Mecklenburg Bay, this figure was 38% (17–60%). High inter-individual variability in the heat production rate was also observed. Only the resting metabolic rate (level without locomotor activity) was used for calculations. It corresponded to the mean value calculated for areas under the smooth lines between activity peaks.

The specific metabolic rates of *I. chelipes* from the Gulf of Gdansk and Mecklenburg Bay were significantly ($P < 0.05$) related to specimen wet weight. The relationship was described within the experimental mass range by the power functions $\mathrm{SMR}_1 = 0.53\mathrm{ww}_1^{-0.56}$ ($R = -0.48$) for animals from the Gulf of Gdansk and $\mathrm{SMR}_2 = 0.32\mathrm{ww}_2^{-0.75}$ ($R = -0.63$) for those from Mecklenburg Bay (Fig. 2).

The mean specific metabolic rates of *I. chelipes* from the Gulf of Gdansk and Mecklenburg Bay were $7.5 \pm 3.4\,J\,h^{-1}\,g^{-1}$ ww ($n = 28$) and $8.4 \pm 2.6\,J\,h^{-1}\,g^{-1}$ ww ($n = 28$), respectively. When specific metabolic rates of specimens from both sites were compared concerning the mass,

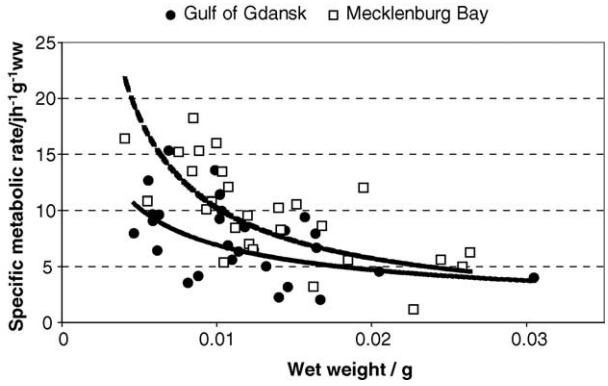

Fig. 2. Relationships between metabolic rate and wet weight of *I. chelipes* from the Gulf of Gdansk (solid line) and Mecklenburg Bay (dashed line).

Table 1
Wet weight and specific metabolic rate of males and females from the Gulf of Gdansk and Mecklenburg Bay

	The Gulf of Gdansk		The Meckenburg Bay	
	Males	Females	Males	Females
Number of animals	13	15	13	15
Wet weight (g)				
Minimum	0.005		0.008	
Maximum	0.015		0.036	
Mean (±S.D.)	0.013 ± 0.007	0.010 ± 0.003	0.018 ± 0.009	0.011 ± 0.004
Specific metabolic rate ($J\,h^{-1}\,g^{-1}$ ww)				
Minimum	2.0	4.2	1.2	3.2
Maximum	15.5	13.6	18.2	16.4
Mean (±S.D.)	6.5 ± 3.9	8.4 ± 2.6	8.8 ± 4.8	10.5 ± 3.8

a statistically significant difference ($P < 0.05$) occurred only in the smallest animals studied from 0 to 0.01 g weight range (Fig. 3). The values were $9.2 \pm 3.9\,J\,h^{-1}\,g^{-1}$ ww ($n = 10$) and $14.0 \pm 2.9\,J\,h^{-1}\,g^{-1}$ ww ($n = 9$) for *I. chelipes* from the Gulf of Gdansk and Mecklenburg Bay, respectively.

The specific metabolic rate of females ($n = 15$) from the Gulf of Gdansk with an average wet weight of 0.010 ± 0.003 g (0.005–0.016 g) ranged from 4.2 to $13.6\,J\,h^{-1}\,g^{-1}$ ww (average (av.) $8.4 \pm 2.6\,J\,h^{-1}\,g^{-1}$ ww), whereas that of males ($n = 13$) with an average wet weight of 0.013 ± 0.007 g (0.006–0.030 g) ranged from 2.0 to $15.3\,J\,h^{-1}\,g^{-1}$ ww (av. $6.5 \pm 3.9\,J\,h^{-1}\,g^{-1}$ ww) (Fig. 4). Females from Mecklenburg Bay ($n = 15$) with an average wet weight of 0.011 ± 0.004 g (0.004–0.018 g) exhibited metabolic rates in the range of $3.2–16.4\,J\,h^{-1}\,g^{-1}$ ww (av. $10.5 \pm 3.8\,J\,h^{-1}\,g^{-1}$ ww). Males from this region ($n = 13$) of an average wet weight of 0.018 ± 0.009 g (0.008–0.036 g) had values from 1.2 to $18.2\,J\,h^{-1}\,g^{-1}$ ww (av. $8.8 \pm 4.8\,J\,h^{-1}\,g^{-1}$ ww). The differences between the sexes were not statistically significant ($P > 0.05$) (Table 1).

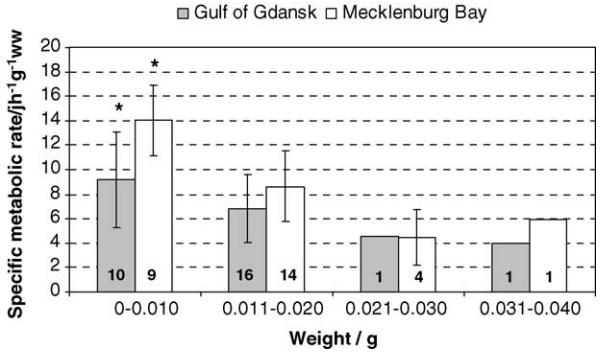

Fig. 3. Comparison of the specific metabolic rates (mean ± S.D.) of *I. chelipes* in different weight ranges from the Gulf of Gdansk and Mecklenburg Bay. Numbers inside the bars indicate the numbers of specimens and stars indicate statistically significant differences.

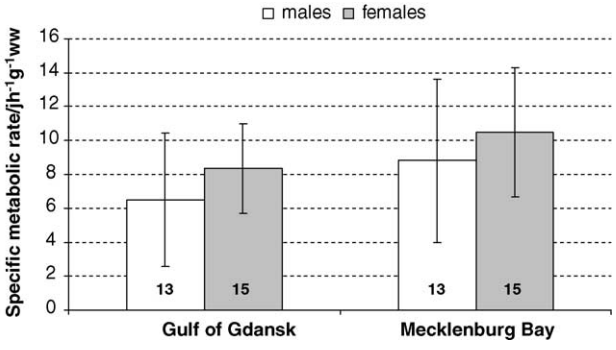

Fig. 4. Mean metabolic rates (±S.D.) of male and female *I. chelipes* from the Gulf of Gdansk and Mecklenburg Bay. Numbers inside the bars indicate the numbers of specimens.

4. Discussion

The current observations of *I. chelipes* under laboratory conditions showed that this species exhibits a rather low degree of locomotor activity. It spent most of its time sitting and feeding on *Enteromorpha* filaments. Swimming specimens were observed sporadically. During calorimetric measurements it was easy to distinguish periods of locomotor activity based on peaks. *I. chelipes* exhibited different levels of locomotor activity and the highest and the lowest ratio between resting and active metabolic rates for specimens from Gulf of Gdansk were 1:4.4 and 1:1.4, respectively, and for those from Mecklenburg Bay 1:2.5 and 1:1.2, respectively. It should be kept in mind that the behavior exhibited by animals under laboratory conditions might differ from that in the natural habitat. The values obtained in the current study concur with those reported by Willmer et al. [17], who found that the ratio between the basal and maximum metabolic rates in invertebrates vary in the range of 1:2 to 1:10. The active metabolic rate in *Idotea balthica* at 20 °C was three times higher than the resting one [18]. Normant et al. [19] found the highest ratio in the Baltic amphipod *Gammarus oceanicus* to be 1:2.4.

The metabolic rates of males and females of *I. chelipes* did not differ significantly. It is most probable that it is not sex but the physiological state of an organism that might affect the metabolic rate. It would be interesting to investigate

ovigerous females; unfortunately, since the samples were collected at the end of the breeding season in August, none were found [16]. In general, weight is the factor that significantly affects the metabolic rate of an organism. Similar conclusions were drawn by Normant et al. [20,19], who found that differences in the specific metabolic rates between males and females of *Saduria entomon* and *G. oceanicus* belonging to the same length classes were probably caused by differences in wet weight. However, there is little information in the literature on the sex effect on the total metabolism of crustaceans [21].

The metabolic rate of *I. chelipes* determined by direct calorimetry was significantly higher than that recorded with respirometry by other researchers. In order to permit comparison with values from the literature, those from the current study were recalculated with the Gnaiger and Forstner [22] conversion factor of 1 ml O_2 = 20.08 J. When recalculated into dry weight units, the mean specific metabolic rates of specimens from the Gulf of Gdansk and Mecklenburg Bay were $27.3 \pm 11.7\ J\ h^{-1}\ g^{-1}$ dw and $34.4 \pm 15.6\ J\ h^{-1}\ g^{-1}$ dw, respectively. For the same species from the brackish water pools at Scarlett Point, Isle of Man, this value was $17.0\ J\ h^{-1}\ g^{-1}$ dw [23]. For *I. baltica* and *Idotea emarginata* from the coastal waters of Helgoland (North Sea) they were $13.5\ J\ h^{-1}\ g^{-1}$ dw and $12.6\ J\ h^{-1}\ g^{-1}$ dw, respectively [24]. The differences in the metabolic rates probably stem from the lower experimental temperatures applied by Jones [23] and Salomon and Bucholz [24] that were 8 and 5 °C, respectively. The total metabolic rate of *I. chelipes* was similar compared to that of the other brackish water species like *G. oceanicus* and *Gammarus tigrinus*, which were $5.7 \pm 2.2\ J\ h^{-1}\ g^{-1}$ ww (at 15 °C) and $4.7 \pm 1.2\ J\ h^{-1}\ g^{-1}$ ww (10 °C), respectively [25,19].

The exponents "*b*" in the power functions for the relation between the weight specific metabolic rate and the weight itself are low in specimens from Mecklenburg Bay ($b = 0.25$ or $b - 1 = -0.75$) and the Gulf of Gdansk ($b = 0.44$ or $b - 1 = -0.56$). The values obtained are much lower than Kleiber's predictions, in which the exponent *b* should be in the range of 0.67–1 [26]. The low exponent values indicate that the metabolic rate is neither related to body surface nor volume. In his studies on the respiratory metabolism of *I. balthica*, Bulnheim [18] obtained a much higher value ($b = 0.68$), which was in the proper range. On the other hand, there are many examples in which the exponents were also low. Bridges and Brand [27] reported that the respective exponents *b* of 0.49 and 0.48 recorded for the decapods *Panulirus interruptus* and *Hommarus gammarus* were probably depressed by higher activity. The lower exponent value ($b = 0.55$) in the amphipod *Gammarus oceanicus* was explained by the low metabolic rates of the largest specimens, which were not completely dependent on mass, but were rather due to organism age [19]. Other reasons also tend to decrease the value of allometric exponent b, such as the parasitic infections that were observed in the bivalve *Pisidium amnicum* [28].

Since *I. chelipes* belongs to the fauna of brackish water origin, it might be assumed that it lives under favorable osmotic conditions in the Baltic Sea. According to Remane and Schlieper [4], organisms living under optimal environmental conditions are characterized by the lowest metabolic rates (energetically most profitable). However, *I. chelipes* is a brackish water species, which, at a salinity of 7 psu, maintains haemolymph osmotic concentration at a higher level than that of the external environment [11,29]. This process requires additional energy. The difference between internal and external concentrations decreases as salinity increases. Therefore, the assumption might be made that the metabolic rates of specimens from the Gulf of Gdansk are higher than those of the Mecklenburg specimens due to osmoregulation costs. However, the results obtained contradict this hypothesis. Moreover, the smallest specimens from the 0 to 0.001 g wet weight range inhabiting Mecklenburg Bay are characterized by higher metabolic rates. Remane and Schlieper [4] stated that animals from brackish waters are characterized by lower water permeability of their body membranes in comparison to specimens inhabiting more saline water decreasing the cost of energy spent in the osmoregulation process. Additionally, high inter-individual variability in heat production rates was observed in this group. This is difficult to explain, especially since significant differences in metabolic rates between the two populations were not noted among specimens from the 0.011 to 0.040 g wet weight range. One of the reasons might be that the difference in salinity between the two regions was 5 psu, which, presumably, was not enough to cause significant changes in the metabolic rates of *I. chelipes*. Similar observations were made with regard to *G. oceanicus*, a species of marine origin that inhabits the brackish waters of the Baltic Sea and was acclimated to five different salinities ranging from 5 to 30 psu [19,30]. It is also possible that differences in metabolic rate do not occur. Jones [23] demonstrated that *I. chelipes* from British brackish waters that were exposed to a salinity range of 10–100% of seawater exhibited a steady rate of oxygen consumption. Some studies have shown that the evaluation of changes in oxygen consumption rates does not provide reliable information regarding the energy costs of osmoregulation because the anaerobic metabolism involved in intracellular osmoregulation is not detected [31–34]. This refers especially to studies on salinity effects. Not only does the salinity differ in the two regions studied, but there are also many other biotic and abiotic parameters in the Gulf of Gdansk and Mecklenburg Bay that are significant to the functioning of these regions' inhabitants. Although they might cause changes in the biology, ecology or even the physiology of this species, they have no significant effect on the metabolic rate. More detailed studies on the comparative physiology and genetics of *I. chelipes* would provide more information. There are examples in the literature of the genetic adaptation to local habitats of different populations of the same species living at different salinities [35,36].

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