Respiratory metabolism of *Idotea balthica* (Crustacea, Isopoda) in relation to environmental variables, acclimation processes and moulting

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KURZFASSUNG: Der respiratorische Stoffwechsel von *Idotea balthica* (Crustacea, Isopoda) in Beziehung zu Umweltfaktoren, Anpassungsvorgängen und zum Häutungsgeschehen. Der Atmungsstoffwechsel der euryhalinen Meeresassel *Idotea balthica* (Pallas) wurde in Abhängigkeit von der Körpergröße, der Temperatur und dem Salzgehalt untersucht. Die auf elektrochemischem Weg durchgeführten Messungen des Sauerstoffbedarfs ergaben eine nahezu gleichmäßige Erhöhung der Stoffwechselintensität mit zunehmender Temperatur. Gegenüber dem Ruheumsatz steigt der Aktivitätsstoffwechsel bei allen getesteten Temperaturen (5°, 10°, 15°, 20° C) ungefähr um das 3- bis 4fache. Die größenbezogenen Stoffwechselrelationen zeigen eine deutliche Abhängigkeit von der Salinität. Der zeitliche Verlauf der Anpassungsvorgänge nach einem Temperatur- und Salinitätsstreß wurde bis zum Erreichen eines neuen, gleichbleibenden Stoffwechselniveaus verfolgt. Die Adaptation nach einem plötzlichen Temperaturwechsel (Überführung von 15° in 5° C und von 5° in 15° C) ist innerhalb weniger Stunden vollzogen. Ein abrupter Salinitätswechsel von 30 in 10 ‰ hat einen wesentlich längeren und mit einem erheblichen Stoffwechselanstieg verknüpften Anpassungsvorgang zur Folge als ein Salzgehaltssprung in umgekehrte Richtung. Ferner wurden die Änderungen des Sauerstoffbedarfs während der Häutung, die sich in zwei räumlich und zeitlich getrennten Abschnitten vollzieht, untersucht. Der Sauerstoffverbrauch adulter Individuen ist über einen Zeitraum von ca. 40–80 Stunden (bei 15° C) erhöht und weist während des Abwurfs des alten Exoskeletts einen zweigipfligen Anstieg auf, der etwa das Dreifache der Normalwerte erreicht. Verschiedene physiologische Aspekte werden unter Einbeziehung ökologischer Gesichtspunkte, die sich insbesondere auf das vorwiegend sublitorale Vorkommen von *I. balthica* beziehen, erörtert.

INTRODUCTION

The representatives of the isopod genus *Idotea* inhabit mainly marine littoral zones. Along the German coasts six different *Idotea* species have been recorded (Gruner 1965); of these, *Idotea balthica* represents one of the most common forms which may be found locally in high abundance within sublitoral algal belts and eelgrass-meadows. Its significant population densities convey to *I. balthica* considerable importance in the energy flow through littoral ecosystems. On the one hand, it participates in the utilization of the primary production in the sea and, on the other hand,

it serves as food for several other marine animals, especially for fishes. Although the members of the genus *Idotea* are potentially omnivorous scavengers, seaweeds, eel-grass and floating vegetable debris provide the main food source in their particular habitat (NAYLOR 1955). This is also reflected by the observation that, to some extent, several *Idotea* species are closely associated with certain benthonic algae.

Various aspects of the ecology and general biology have been thoroughly studied in several *Idotea* species. However, as pointed out by JONES (1974), contributions to the physiology of this genus are still limited. Among the physiological subjects studied some investigations have been undertaken on activity patterns (JANSSON & KÄLLANDER 1968, HØRLYCK 1973a), heat resistance (FURCH 1972), osmoregulatory capacities (TODD 1963, HØRLYCK 1973b) as well as metabolism and energy exchange (Fox & SIMMONDS 1933, STOICOVICA & ROSCA 1958, VON OERTZEN 1965, STRELNIKOVA 1971, KHMELEVA 1973, SHAPUNOV 1973, JONES 1974).

The experiments reported here contribute to the environmental physiology of *Idotea balthica* and complement previous pertinent studies. They were undertaken to test the influences of temperature and salinity on oxygen uptake as related to body size. In addition, the effects of environmental stress, in particular the compensatory reactions following changes of ambient temperature and salinity have been recorded in relation to the time courses of acclimation and the magnitudes of the physiological adjustments. Finally, some data are presented on alterations of metabolic rates during the moulting process.

MATERIALS AND METHODS

Specimens of *Idotea balthica* (PALLAS) were collected in spring and summer in near-shore waters of the Lübeck Bay (Baltic Sea). The salinity in this area averages 15 ⁰/oo. The isopods were sorted from algae and leaves of *Zostera marina*, transferred to the laboratory and maintained in aerated aquaria supplied with a bottom filter. Usually, they were kept at constant temperatures (5°, 10°, 15°, 20° C) for several weeks until use for experiments. In general, brackish water of 10 ⁰/oo S served as culture medium. During summer time, under natural light-dark cycles, the isopods reproduced in the laboratory (at 15° C), but mostly failed to do so during other seasons. *Enteromorpha* sp., pieces of *Mytilus edulis* flesh and commercial fish food ("Tetramin") comprised the diet offered.

Idotea balthica is subdivided into several subspecies. On the coasts of western and northern Europe four allopatric subspecies (or geographical races) have been recorded, which are both morphologically and ecologically separated from each other. On the basis of the descriptions given by TINTURIER-HAMELIN (1963) the specimens found in the Lübeck Bay were assigned to *Idotea balthica balthica*.

The respiratory rates were measured by a flow-through polarographic technique providing continuous pO_2 determinations. The experimental set-up used has been described in detail in a publication dealing with investigations on the metabolism of *Gammarus* species (BULNHEIM 1972).

The whole experimental system consisted of a respirometer and a recording unit.

A pump (Unita II b, Braun, Melsungen) continuously forced a constant flow of air-saturated water through the glass respirometer. The animal chamber inserted in this system was adjusted to the size of the test organisms. In combination with a magnetic stirrer, a Clark-type electrode determined dissolved oxygen in the aqueous solution. The electrode employed consisted of a platinum cathode, protected from the sample being measured by thin membranes of cellophane and Teflon, and a silver-silver chloride reference electrode. 0.5 m KCl solution served as an electrolytic agent. The electrode operated in conjunction with an oxygen analyser (Eschweiler & Co, Kiel) and a "Servogor" recorder (Metrawatt, Nürnberg). The readout was in millimetres oxygen partial tension. Detailed references to calibrations and calculations are given in the afore-mentioned paper.

In order to reduce the activity of the individuals examined, a piece of gauze which meets the thigmotactic behaviour of the idoteids was inserted in the respiration chamber. Measurements of single specimens were conducted in the respirometer submerged in a temperature-controlled water bath at 5°, 10°, 15°, and 20° C $\pm$ 0.1° C in media of 10 $^0/_{00}$ and 30 $^0/_{00}$ S, respectively. Prior to experimental use the test animals were starved for one day. They remained in the respiration chamber until constant oxygen-uptake rates were obtained. In general, the values recorded during the first two hours of the pO_2 determinations were discarded. Before and after each run, and additionally during long-term recordings, control measurements (without test animals) were performed. The flow of water through the respirometer was adjusted such that the isopods generally consumed less than 10 $^0/_0$ of the available oxygen.

RESULTS

Oxygen consumption and size

In poikilotherms, the dependence of oxygen consumption on body size has been verified by many investigators (cf. Hemmingsen 1960). In most cases this relationship is not linear; rather, the oxygen-uptake rates represent an exponential function of body weight. Therefore, an adequate characterization of the specific metabolic levels of a given poikilothermic animal species requires determinations of respiratory rates as a function of size.

The mathematical expression of metabolism per unit time is given by the allometric formula: $y = a \cdot x^b$, where $y = O_2$ consumption, $x =$ weight, a and $b =$ constants. The regression coefficient b indicates the slope of the logarithmic plot of oxygen consumption versus body weight and the parameter a expresses the intercept on the Y-axis. This plot gives a straight line with a positive slope; a negative slope results, when weight-specific respiration is calculated, whereby the equation assumes the form $y/x = a \cdot x^{b-1}$.

In several isopod species, the effects of various environmental factors on metabolism have been examined. However, relatively few publications are devoted to their influences on the relationships between rates of oxygen uptake and body size. In *Idotea balthica*, first the effects of various temperature levels – 5°, 10°, 15°, and 20° C

— on respiration were studied. The temperature range selected corresponded fairly well to the thermal regime which the idoteids normally encounter in their habitat.

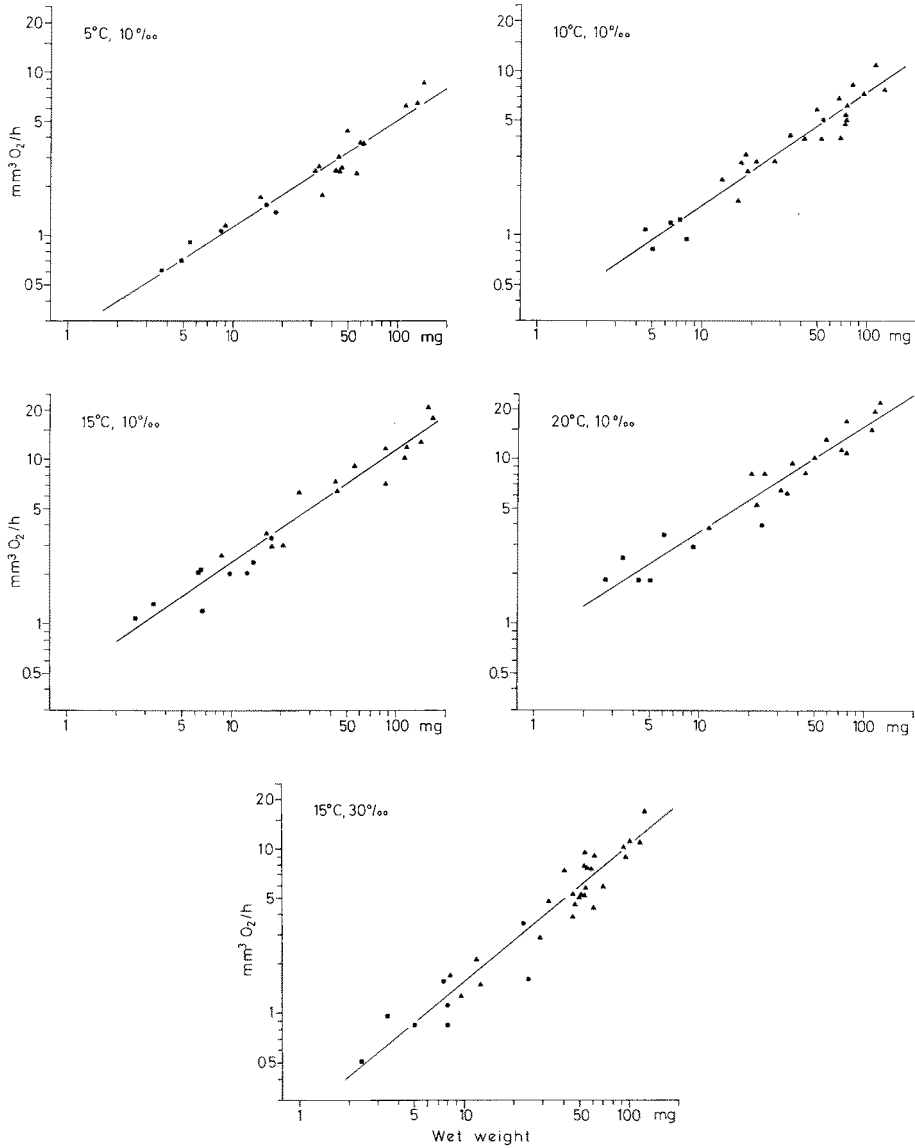In general, the test animals were pre-exposed to each experimental temperature

Fig. 1: *Idotea balthica*. Relationships between oxygen uptake and size at four different temperatures and two salinities. Symbols: ■ juveniles, ● females, ▲ males. The respective values computed for determination of levels and slopes of the regression lines (parameters *a* and *b* as well as their standard errors) are listed in Table 1

for several weeks, at least for a minimum of 5 days. In addition to the experiments conducted at a salinity of 10 ⁰/₀₀, oxygen determinations were also performed at 30 ⁰/₀₀ and 15° C. The results obtained from these investigations were intended to serve as a basis for the studies on acclimation processes to be described later.

Figure 1 illustrates the relationships between oxygen consumption and body size as related to temperature and salinity; Table 1 summarizes the corresponding data calculated which are supplied with further parameters necessary for statistical analysis. As can be seen from this figure, the values measured scatter to some extent about the

<div align="center">Table 1</div>

Idotea balthica. Data calculated for characterizing oxygen consumption $(mm^3 O_2/g/h)$ as a function of body size in relation to temperature ($^\circ$ C) and salinity (‰). a = intercept of the regression line on the Y-axis indicating oxygen uptake per unit weight (1 g wet weight), b = regression coefficient, $s_y \cdot x$ = standard error of the y values for a given value of x, r = coefficient of correlation, n = number of specimens measured

$^\circ$ C	‰	a	b	$s_y \cdot x$	r	n
5	10	22.54 ± 1.15	0.64 ± 0.04	0.080	0.97	21
10	10	35.22 ± 1.15	0.68 ± 0.04	0.087	0.96	27
15	10	56.80 ± 1.15	0.69 ± 0.04	0.095	0.97	24
20	10	68.18 ± 1.17	0.63 ± 0.04	0.098	0.95	23
15	30	67.52 ± 1.16	0.81 ± 0.04	0.105	0.96	34

regression lines reflecting individual variation. Most of the test animals chosen were males; only few, non-reproducing females were used. Since no differences between the sexes appeared to occur, the respiratory data for males and females were pooled for regression analysis.

The high levels of the coefficients of correlation calculated clearly document the dependence of respiratory rates on body size. The different thermal regimes exert a marked effect on the rates of standard metabolism indicating an almost continuous rise with increasing temperature. From the data presented, rate-temperature curves as well as Q_{10} values may be calculated. Such procedure has been omitted, since slight differences of these values between various size groups are expected to result as a consequence of the diverse regression coefficients obtained. The latter show significant differences in the slopes of the log weight – log oxygen uptake regression lines, when the rates are compared between 30 and 10 ⁰/₀₀ ($p < 0.05$). In 10 ⁰/₀₀ metabolic rates are higher than in 30 ⁰/₀₀; however, the regression lines converge at the end of the weight range tested. In contrast to the rather high level of the regression coefficient obtained at 30 ⁰/₀₀, the b values calculated from the measurements in media of 10 ⁰/₀₀ range approximately between 0.6 and 0.7; thus they reflect rather close proportionality of metabolism to body-surface area which is indicated by an exponent of 0.67.

The slopes of the regression lines obtained at 10 ⁰/₀₀ and the four temperature regimes examined were compared with one another for testing significances. The statistical treatment of the data by employing analysis of covariance did not reveal significant differences ($p > 0.2$) between the various regression coefficients.

In respiratory studies it is importance to distinguish between standard and active

metabolic rates. On the basis of the characteristic patterns obtained during the continuous pO_2 monitoring and including visual inspections of the isopods examined in the respirometer, it was possible to differentiate between active and standard metabolism and to evaluate the level of activity to some degree. Between the two rates corresponding to maximal and minimal activity, various levels of routine rates may be distinguished. During the experiments conducted, activity effects due to locomotion were largely excluded by the small sizes of the respiration chambers used and the substratum provided to which the idoteids were attached. Due to the quiscent behaviour of most specimens tested, maximum values could be measured in only a few cases. Accordingly, regression coefficients relating to active metabolism have not been calculated. However, some tentative values on the scope for activity, i.e. the difference between standard and active rates of metabolism (FRY 1957), could be obtained, although it is not certain whether the respiratory data recorded of active specimens represent maximal rates which might occur under natural conditions. Some recordings have shown that, during periods of extreme excitement, the activity rates measured exceed standard rates by approximately four times at 10° and 15° C. Values nearly three times the standard rates have been obtained, on the other hand, at 5° and 20° C, but there is some evidence that they are too low. This approach of estimating activity metabolism only refers to adult specimens; it cannot be excluded that some size-dependent differences exist in this respect. This aspect should be examined more precisely by employing adequate methods to measure oxygen uptake and activity simultaneously.

Metabolic responses following environmental stress

Temperature stress

Many poikilotherms are known to be able to compensate for changes in temperature conditions which they are exposed to (for review, see PRECHT et al. 1973). Although several investigations have been performed testing the capacity for temperature acclimation in crustaceans, only few studies, however, have taken into account the time course of this compensatory adjustment.

The following experiments were carried out in order to study the time required for transition from one acclimation state to another. Adult males of *Idotea balthica*, acclimated under laboratory conditions to two different temperature regimes, 5° and 15° C, respectively, were subjected to sudden changes of temperature. Figures 2 and 3 illustrate the results of these experiments. A sudden transfer of warm acclimated animals from 15° to 5° C led to a new metabolic steady state within ca. 3 hours. The oxygen-uptake rates measured thereafter roughly corresponded to the rates of long-term acclimated isopods to 5° C (cf. Fig. 1). The high rates initially recorded may have been partially caused by disturbances which the test animals had experienced due to the transfer into the respiration chamber.

A similar response was found in the second set of experiments, the abrupt exposure of cold acclimated individuals from 5° to 15° C. On the average, the time

course until attaining a new metabolic level at the altered temperature lasted approximately 15 hours. After the thermal stress a slight decrease of respiration rates occurred indicating that for a while at the elevated temperature the test animals were in a
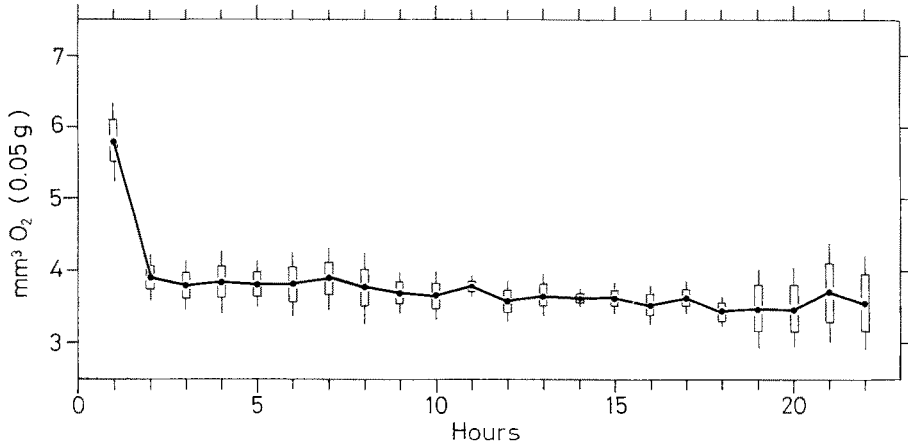

Fig. 2: *Idotea balthica.* Time course of acclimation in adult ♂ ♂ (corrected to 0.05 g body weight) following sudden transfer from 15° to 5° C (n = 4). Vertical lines: standard deviation; vertical bars: standard error of the mean
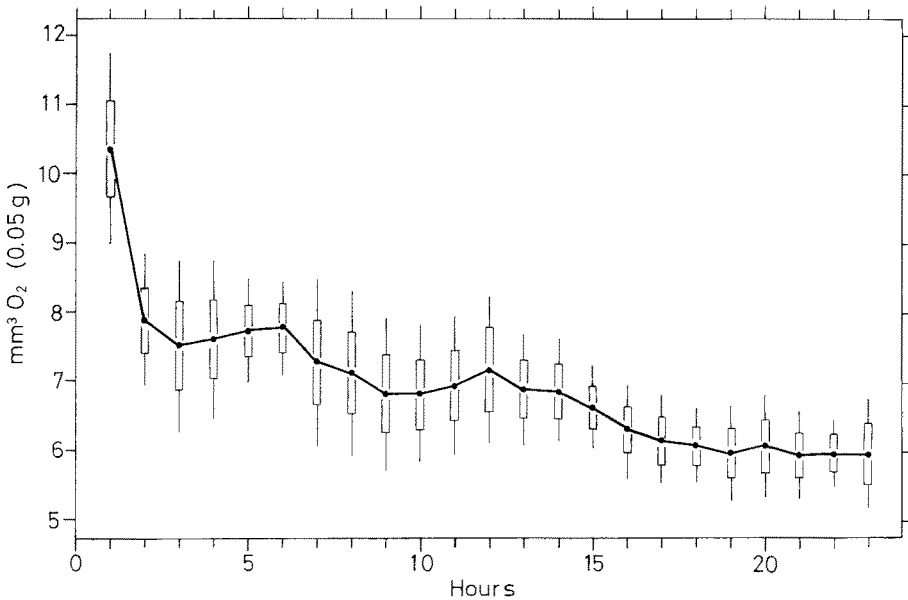

Fig. 3: *Idotea balthica.* Time course of acclimation in adult ♂ ♂ (corrected to 0.05 g body weight) following sudden transfer from 5° to 15° C (n = 4). Vertical lines: standard deviation; vertical bars: standard error of the mean

somewhat excited state which slowed down after they had been undisturbed for several hours in the respirometer. This also became apparent in further experiments with specimens of different size. In conclusion, thermal acclimation has no significant effect on the rate-temperature relations of respiratory metabolism in *I. balthica*.

Salinity stress

Idotea balthica tolerates a wide salinity range. SEGERSTRÅLE (1947) noted that it occurs in the northern Baltic Sea in salinities as low as 3.5 °/oo and SYWULA (1964) reported a minimum mean salinity tolerance of about 4.25 °/oo. Inhabiting brackish as well as sea water, *I. balthica* is distributed on both European and American coasts. Generally, it prefers localities with clear and continuously renewed water, but avoids environments associated with strong salinity fluctuations. The tolerance to a wide salinity range is based on well-developed osmoregulatory capacities. As demonstrated by HØRLYCK (1973b), *I. balthica* exhibits a hyperosmotic regulation which is in accordance with the mode of osmoregulation in other euryhaline *Idotea* species investigated.

The experiments conducted follow a design that was applied in studies on adaptation to changes of environmental salinity in several euryhaline *Gammarus* species (BULNHEIM 1972). After long-term acclimation to salinity of 10 °/oo, individuals of *I. balthica* were suddenly exposed to a salinity level of 30 °/oo and vice versa. During these studies oxygen-consumption rates of adult individuals were first measured for at least 7 hours at the external concentration to which they were acclimated for a long period of time. Thereafter, they were subjected to a sudden rise or fall of ambient salinity, without modifying the conditions of oxygen measurement. The responses following osmotic stress were continuously monitored until new steady levels were obtained. The relative oxygen-uptake rates expressed in Figures 4 and 5 refer to the percentages of increase or decrease in respiration rates compared with the metabolic levels which occurred before the salinity was altered.

An abrupt change from 10 to 30 °/oo led to some decrease of the oxygen consumption (Fig. 4). After an initial overshoot the metabolic reaction settled down to a new stabilized rate within 4 to 6 hours following the salinity change. Thereafter, the oxygen uptake was reduced by about 10 °/o in relation to the preceding metabolic activity. Since during the next few hours no further alterations occurred – except for some minor fluctuations – the period of compensatory adjustment is considered to be rather short. It should be pointed out that this finding of reduced O_2 uptake in 30 °/oo is in accordance with the above presented results on oxygen-consumption rates versus body weight as influenced by salinity (cf. Fig. 1).

In contrast to the transfer from a more dilute to a more concentrated medium, a quite different response could be ascertained when the opposite experiment was performed. A sudden salinity fall from 30 to 10 °/oo also induced an initial overshoot which was associated with a rather long period of maintaining an increased oxygen uptake (Fig. 5). For about 20 hours following the osmotic stress, oxygen-consumption rates were elevated on an average of 40 °/o. Thereafter, during the next 10 hours, the

metabolic rates gradually decreased until attaining a new steady state, which was slightly higher than it was before exposure to the salinity stress. Thus, the whole process of physiological compensation associated with the salinity change from 30 to 10 %₀ required ca. 30 hours. Compared with the results of the first set of the salinity experiments and, in addition, taking into consideration observations of the test animals, there is good reason to suspect that the raised oxygen-uptake rates can be attributed to the compensatory reaction rather than indicating a high level of spontaneous activity.
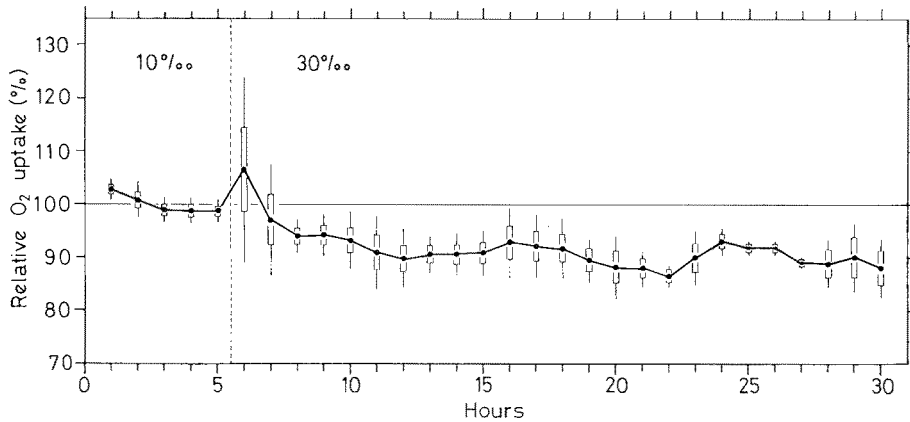

Fig. 4: *Idotea balthica*. Time course of salinity acclimation ($\male\,\male$, ca. 0.05 g) following abrupt change from 10 to 30 ‰ S at 15° C (n = 5). Vertical lines: standard deviation; vertical bars: standard error of the mean

Fig. 5: *Idotea balthica*. Time course of salinity acclimation ($\male\,\male$, ca. 0.05 g) following abrupt change from 30 to 10 ‰ S at 15° C (n = 5). Vertical lines: standard deviation; vertical bars: standard error of the mean
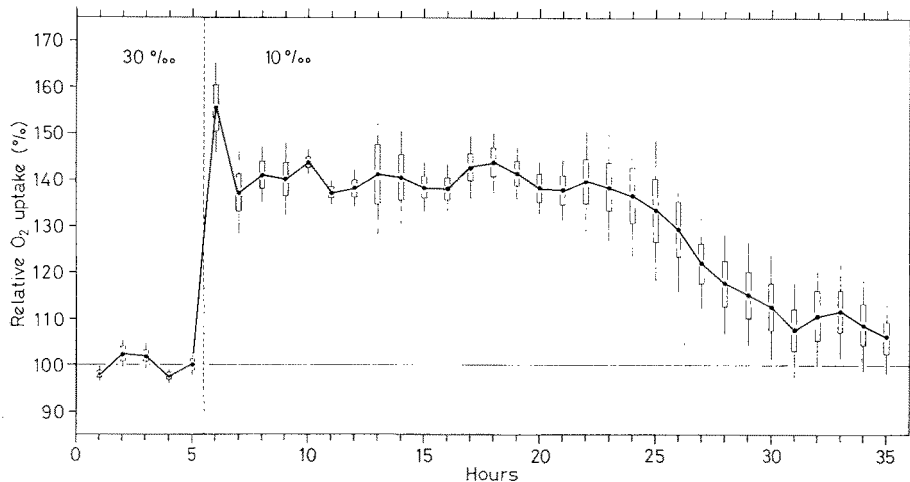
Metabolic changes during moulting

All crustaceans grow through periodic shedding of the exoskeleton. The process of moulting is associated with various morphological, physiological and biochemical changes which have received special attention in decapods (PASSANO 1960). In isopods, however, little is known on metabolic alterations related to moulting and on the role of endogeneous and exogeneous factors controlling this process. Thus far only WIESER (1965) has reported on changes of respiratory rates during moulting in the woodlouse *Porcellio scaber*.

The representatives of the order Isopoda are characterized by a bipartite exuviation. During the first phase of moulting the integument is split between the fourth and fifth thoracic segment providing in the first instance the withdrawal of the old cuticle from the last thoracic segments and the abdomen. Temporally separated from this ecdysis posterioris, at a later date exuviation of the anterior body part, the ecdysis anterioris, is accomplished. In reproducing females, during the interphase between both moultings, copulation takes place. The duration of this phase is dependent on temperature and size. Observations made in adult specimens of *Idotea balthica* revealed an interphase period of 15 hours (♀, 13 mm body length, 15° C), 17 hours (♂, 15 mm body length, 15° C), and 10 hours (♂, 17 mm body length, 20° C). Taken all together, the respiratory alterations during moulting were measured in six individuals; however, in three of them these studies could not be accomplished throughout the whole process of ecdysis.
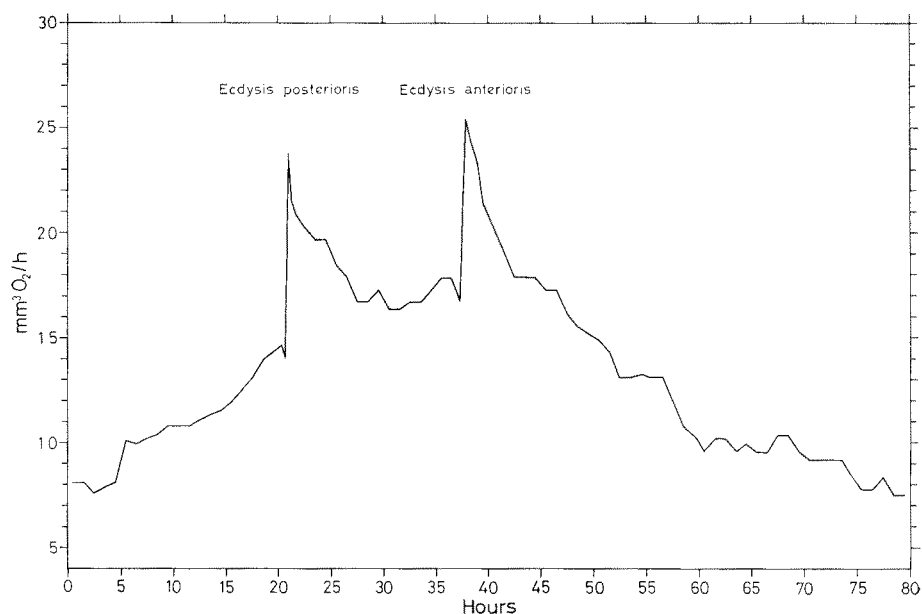

Fig. 6: *Idotea balthica.* Respiratory alterations associated with moulting
(♂, 0.054 g, 15° C, 10 ‰)

The continuous monitoring of oxygen-consumption rates during moulting has clearly shown that the changes of metabolic rates recorded correspond to the two exuviation phases (Fig. 6). At the end of the premoult stage, about 8–15 hours prior to the posterior ecdysis (at 15° C), a gradual increase in the rate of oxygen uptake could be noted; sometimes it was intensified by periods of activity bursts. When the withdrawal from the posterior part of the old exoskeleton was effected, a sharp rise in oxygen consumption appeared. Thereafter, a decline of the oxygen demand occurred, although elevated rates were maintained at an almost constant or slightly decreasing level. The interphase is terminated by a second sharp peak reflecting the moult of the anterior body part. Finally, a gradual decline of oxygen-consumption rates ensued until normal values, corresponding more or less to premoult levels, were reached. This period required approximately the same time as the corresponding process of premoult. As related to adult individuals ($>$ 10 mm body length) and a temperature of 15° C, the whole phase of increased metabolic requirements during moulting was shown to comprise a period of ca. 40 to 80 hours. It is dependent on temperature and body size: decreasing temperature and increasing size cause a temporal prolongation of the whole process.

On average, the two peaks of which the second was found to be generally somewhat higher than the first one exceeded standard rates about three times, whereas in the interphase the rise of metabolic rates was about twice the standard values. The sharp peaks during exuviation appeared to be caused by short bursts of intense activity in the course of which, within a few minutes, the act of shedding was accomplished. The high oxygen demand during the interphase, on the other hand, was not related to such excitatory behaviour, since the test animals generally spent most of their time in an inactive state. Hence, it appears to be a consequence of the absorption of water and other physiological processes associated with moulting.

According to the cyclic structural changes of the skeleton and other characteristics, the intervals between the moults may be subdivided into several intermoult stages. The criteria established by Drach (1939) for decapods have been applied to isopods in a slightly modified form (Stevenson 1961, Wieser 1965). In the course of these studies it became obvious that – except for the late premoult and early postmoult stages – resting metabolism measured in intervals during an individual intermoult cycle did not reveal further significant variations.

In this connection, it appears to be of some interest to include some data on the moulting frequency in *Idotea balthica*. Although only few data have been gathered, evidence was provided that in males subsequent intermoult stages recur with progressively longer duration. It was found, that the intermoult cycle of males at a body length of 10 mm averages 2–3 weeks and that of 20 mm sized males averages 4 weeks maintained at 15° C and 10 %o. On the other hand, in females a scattering of the moulting frequency was observed; moreover, it could not yet be clarified if there exist differences between females in reproductive or resting stages, respectively.

DISCUSSION

Many factors are known to affect the rate of respiration in poikilothermic animals. They involve body size, activity, temperature, oxygen concentration, nutritive

conditions and other variables. Some of these exogenous and endogenous factors have been shown to be interdependent and hence, it may be difficult to assess their relative importance on oxygen-uptake rates.

The above results on the relationships between oxygen consumption and body size in *Idotea balthica*, as related to temperature and salinity, demonstrate such environmental influences. The different levels and slopes of the regression lines indicate the extent to which external conditions can affect metabolism. Variations in the regression coefficients due to environmental factors such as temperature and salinity are well documented in crustaceans (DEHNEL 1960, McFARLAND & PICKENS 1965, BULNHEIM 1972) and other invertebrates. Similar to *Idotea balthica*, relatively higher regression coefficients were also found in several euryhaline *Gammarus* species, when a comparison was made between oxygen-uptake rates in more concentrated and more dilute external media. The *b* values obtained in this study correspond to most of the regression coefficients calculated for other crustaceans including isopods (WOLVEKAMP & WATERMAN 1960); generally they are between 0.67 and 1, indicating a range between surface-related and weight-related respiration.

The results reported demonstrate that, within the range tested, neither resting nor active metabolism of *I. balthica* remains thermally insensitive. This is in contrast to the findings obtained from various intertidal invertebrates including crustaceans whose active and standard metabolic rates may be affected by temperature differently (NEWELL 1969, 1973). In most instances, the active rate of respiration has been shown to be markedly temperature-dependent, whilst the standard rate of quiescent animals reveals a relatively low temperature coefficient. As discussed by NEWELL (1973), there appears to be an ecological pattern in the occurrence of temperature-insensitive respiratory metabolism which is evidently confined to intertidal animals. Such homeostasis is of adaptive value to them, since they are frequently subjected to wide and rapid temperature fluctuations. In contrast, subtidal organisms generally do not display temperature independence of metabolism. This conclusion has thus been confirmed by the present investigations on the subtidally occurring *I. balthica*. Furthermore, it was shown in the terrestrial isopod *Porcellio scaber* that standard as well as "excited" and active rates of metabolism are similarly affected by and increase with rising temperature (NEWELL et al. 1974).

Another aspect to be discussed concerns salinity adaptation which involves several physiological and ecological implications. It is a well-documented fact that various euryhaline invertebrates respond to reduced salinity levels by an increase of respiratory rates. This observation does not only apply to *Idotea balthica* but also to *Hemigrapsus oregonensis* (DEHNEL 1960), *Carcinus maenas* (SCHLIEPER 1929, LUCU et al. 1973), *Balanus balanoides* (BARNES et al. 1963), *Gammarus* species (BULNHEIM 1972) and other crustaceans. Moreover, in several marine and brackish-water invertebrates, different patterns of metabolic responses may occur after exposure to salinity alterations; these have been reviewed and classified by KINNE (1971). Several explanations have been put forward regarding the physiological mechanisms that might be responsible for the alterations of the respiratory rates following a decrease or increase of the ambient salinity level. This problem has been critically discussed by POTTS & PARRY

(1964); however, an understanding of the different types and magnitudes of the meta-
bolic responses established is still lacking.

The metabolic alterations following a salinity stress are closely associated with
changes of osmotic and ionic concentrations of extracellular and intracellular body
fluids. Assessing the literature available, only few papers contain information on the
time courses of salinity acclimation as related to respiratory rates, osmoconcentrations
and other processes involved.

The periods of acclimation in crustaceans, which had been exposed to osmotic
stress, were studied, for example, in some decapods (GROSS 1957, SIEBERS et al. 1972,
LUCU et al. 1973), gammarids (BULNHEIM 1972) and in the isopod *Cyathura polita*
(SEGAL & BURBANCK 1963). It is obvious that the time course of such compensatory
adjustments until attaining a new steady state of performance depends on the animal
species examined, the magnitude as well as the direction of salinity change, and other
factors. General conclusions cannot as yet be drawn.

With regard to the temporal relationships of the different functional responses
involved, it is of interest to compare the present data on the alterations of respiratory
rates with the results published by HØRLYCK (1973b) on the time courses of osmotic
adaptation in *I. bathica* and related species. When specimens of *I. balthica* were
transferred from a salinity of 24.5 to 6 %o the freezing-point depression of the haemo-
lymph fell from 1.42° to about 1.0° after one hour (at 10° C); during the next 20
hours it decreased gradually to reach a new steady state with a mean value of $\triangle$° C
= 0.8. When the opposite experiment was undertaken comprising a change from 7 to
25 %o the freezing-point depression rose from 0.71° to about 1.28° within one hour;
during the following 5 hours a new mean steady-state value ($\triangle$° C = 1.38) was
approached.

It is interesting to note that these time courses of acclimation are very similar
to those obtained from the above-reported experiments on the changes of respiratory
metabolism (Figs. 4 and 5), although the levels of the salinity alterations are some-
what different (from 10 to 30 %o and vice versa) when compared with the experimen-
tal conditions of HØRLYCK's study.

Summing up, these results demonstrate that changes from more dilute to more
concentrated external media induce less extensive alterations in rates of oxygen uptake
and lead to a shorter acclimation period than transfers in the opposite direction. In
this regard a parallelism to some euryhaline *Gammarus* species, particularly to *Gam-
marus locusta* must be stressed. As studied by alterations of oxygen uptake in this
amphipod, an abrupt transfer from 10 to 30 %o leads to a new steady state of meta-
bolic rates within 3–5 hours, whereas acclimation following a sudden transfer from
30 to 10 %o takes 30 or more hours (BULNHEIM 1972). The sudden exposure to the
dilute medium which is also associated with an elevated hyperosmotic regulation in
G. locusta causes a significant temporary increase of respiratory rates. In contrast
to this, in *G. duebeni* the corresponding acclimation period takes about 3 hours and
is not accompanied by marked respiratory changes. This difference must be related
to the species-specific environmental requirements of the amphipods concerned. *G.
duebeni* occurs in habitats, especially in the supralittoral zone, characterized by ex-
treme fluctuations of salinity levels and other ecological factors. Like *Idotea balthica*,

Gammarus locusta is preferentially distributed in subtidal localities, but avoids estuaries and other adverse environments tolerated by *G. duebeni*. From this interspecific physiological comparison the patterns of distribution of the species under consideration become more conspicuous. The enhanced oxygen-uptake rates reflect a considerable degree of energy expenditure due to a rapid salinity decline; this suggests that neither *I. balthica* nor *G. locusta* are suited to live in environments where strong salinity fluctuations are likely to occur. On the other hand, the wide occurrence of both species in the Baltic Sea demonstrates that they are able to exist in rather low salinities provided that the concentration of the ambient medium remains fairly constant. In any case, the acclimatory responses obtained indicate that *I. balthica* is better adapted to tolerate rapid temperature changes than sudden salinity alterations.

Before considering the metabolic requirements of moulting, the data of previously published papers pertaining to the metabolism of *Idotea* species should be briefly discussed. It is often difficult to compare published values of oxygen-uptake rates because of differences in the techniques employed, temperatures applied, weight units used, and physiological conditions of the test animals chosen. Hence, the few data reported on oxygen consumption of *Idotea balthica, I. neglecta, I. chelipes (I. viridis), I. emarginata,* and *I. ochotensis* (Fox & SIMMONDS 1933, STOICOVICI & ROSCA 1958, v. OERTZEN 1965, STRELNIKOVA 1971, JONES 1974) cannot be compared adequately with the values presented in this study. Above all, these publications do not refer to rate-size relationships, except for the studies of STRELNIKOVA (1971) and KHMELEVA (1973).

The respiratory rates measured and compared by JONES (1974) in *Idotea neglecta, I. emarginata* and *I. chelipes* reveal only slight differences and are similar to those of other marine peracarid crustaceans. In *I. chelipes,* in contrast to the other two *Idotea* species, an increase of the oxygen demand was noted after exposure to reduced salinity levels.

The alterations in respiratory metabolism displayed during moulting by *Idotea balthica* are similar to those recorded in the woodlouse *Porcellio scaber* (WIESER 1965). At ecdysis, the latter species also shows two peaks of increased metabolic rates which correspond to the exuviations of the exoskeleton being cast in two parts.

In several other crustaceans elevated metabolic requirements have also been measured prior to, or at, ecdysis. This applies to decapods (SCUDAMORE 1947, FROST et al. 1951, BLISS 1953, SCHEER & SCHEER 1954, ROBERTS 1957, HEINEMANN 1964) euphausiids (PARANJAPE 1967) and amphipods (BULNHEIM 1972). In various *Gammarus* species, for example, oxygen consumption increases the standard metabolic rates by 2.2 to 3.9 times during moulting. On the other hand, no such alterations have been detected in the cirripede *Balanus improvisus* variatio *denticulata* (COSTLOW & BOOKHOUT 1958), whereas a low increase, amounting to approximately 32 %, was ascertained in moulting specimens of *Balanus balanoides* (BARNES & BARNES 1963). The data published thus far indicate that in crustaceans oxygen uptake mostly exceeds standard metabolic rates by 2–4 times in the course of this process. The rather long duration of the bipartite moulting in isopods, accompanied by an extended period of elevated oxygen demand implies that exuviations are particularly hazardous events in

their life. This accounts for the observation that, besides failure to complete moulting, unfavourable environmental conditions frequently lead to deaths when approaching or passing ecdysis.

SUMMARY

1. The oxygen uptake of the euryhaline isopod *Idotea balthica* (PALLAS), obtained from the Baltic Sea, was determined by means of flow-through polarography. The rates of respiration were studied in relation to body size, temperature and salinity. Measurements conducted at $5°$, $10°$, $15°$ and $20°$ C in 10 $°/oo$ salinity revealed an almost continuous increase of metabolic rates with rising temperatures. The regression coefficients, calculated for size-dependent respiration, range from about 0.7 to 0.6. Compared with these data, a significantly higher regression coefficient was obtained from determinations made at $15°$ C and 30 $°/oo$. The rates of active metabolism in adult individuals were shown to exceed standard metabolism by approximately 3 to 4 times at all temperatures tested.
2. The compensatory responses following thermal and salinity stress have been recorded in relation to the time courses of acclimation and the magnitudes of the physiological adjustments. Sudden alterations of temperature lead to new steady states of metabolic rates within 3 hours following a change from $15°$ to $5°$ C and approximately within 15 hours following a transfer from $5°$ to $15°$ C. At $15°$ C, an abrupt salinity change from 10 to 30 $°/oo$ and vice versa requires a transition period between successive acclimation states of 6 hours (10 to 30 $°/oo$) and about 30 hours (30 to 10 $°/oo$), respectively. The transfer from the dilute to the more concentrated medium is accompanied by slightly reduced oxygen-uptake rates, whereas the transfer in the opposite direction leads to a marked temporary increase of respiration.
3. The time course and intensity of metabolic changes during moulting were also examined. The exuviations of the posterior and anterior body parts occur temporally separated and are reflected by two peaks of increased oxygen uptake, amounting to approximately three times the standard rates. In the interphase between the successive exuviations an elevated respiratory level is maintained. In adult specimens, the whole phase of increased metabolic requirements during moulting comprises a period from 40 up to 80 hours at $15°$ C.
4. The metabolic requirements and acclimatory responses of *Idotea balthica* are considered in relation to its subtidal habitat and compared with compensatory reactions occurring in some intertidal and supratidal invertebrates. Further physiological and ecological implications are discussed.

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