A COMPARISON OF THE RESPIRATION RATE OF SOME ANTARCTIC ISOPODS WITH SPECIES FROM LOWER LATITUDES

R. A. LUXMOORE*

British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK

ABSTRACT. The oxygen consumptions (R, in $mm^3\ h^{-1}$) of two Antarctic isopods, *Serolis polita* Pfeffer and *Serolis cornuta* Studer, were measured at temperatures ranging from −1.5 to +4.5°C and were found to be related to dry weight (W, in mg) and temperature (t°C) by the equations

$$\ln R = 0.85 \ln W + 0.14\, t - 0.01 \text{ for } S.\ cornuta$$

and

$$\ln R = 0.64 \ln W + 0.07\, t - 1.16 \text{ for } S.\ polita.$$

Activity was shown to increase the metabolic rate by a factor of up to 3.6 and the animals were also found to be susceptible to handling disturbance. This necessitated care with the experimental technique and refinements to the simple sealed-chamber respirometry methods to obtain a reliable estimate of resting metabolic rate. The difficulties of comparing respiratory rates of different organisms, when variations in both environmental temperature and body weight must be taken into account, are discussed and a method is suggested to overcome these problems. Respiratory data for the Antarctic isopods were compared with those of temperate species. They were found to show no evidence of elevation attributable to metabolic cold-adaptation, and appeared to obey the predictions of the Arrhenius equation.

INTRODUCTION

The metabolic adaptions of polar ectotherms to low temperatures have received much discussion (Scholander and others, 1953; Holeton, 1974; White, 1975; Everson, 1977; Houlihan and Allan, 1982; Clarke, 1983), but until recently there has been little experimental data. In the course of a study of the ecology of serolid isopods at Signy Island, South Orkney Islands (60° 43′ S, 45° 38′ W) (Luxmoore, 1982) measurements were made of the metabolic rates of two species. These data were compared with the metabolic rates previously determined for temperate and tropical species of marine isopod.

The metabolic rate of an organism is usually assessed by measuring its oxygen consumption. This is affected by numerous factors, both endogenous, such as body weight, level of activity, stress, reproductive state, feeding, and also external, such as temperature, salinity and photoperiod (Newell, 1970). Consequently, all these factors must be carefully controlled before any meaningful measurement can be taken. The procedure adopted in this study was to estimate the oxygen consumption of an animal in a state of minimal activity with an empty digestive tract. This was termed 'resting metabolism' and is believe to be as close to a measure of 'basal metabolism' as is feasible with marine invertebrates.

The environmental factor which probably has the greatest single effect on metabolic rate in ectotherms is temperature, and experiments were therefore conducted to measure respiration at a variety of temperatures around the normal environmental range of *Serolis*. Since an acute change of temperature can markedly increase the respiration rate, as Bulnheim (1974) has shown for *Idotea baltica*, care

*Present address: International Union for Conservation of Nature and Natural Resources, 219c Huntingdon Road, Cambridge CB3 0DL, UK.

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must be taken to ensure that animals are acclimated over a sufficiently long period, and in this study acclimation lasted from one to three weeks.

Sealed chamber respirometry is very susceptible to errors caused by handling disturbance increasing metabolic rate (Kangas and Lappalainen, 1978). However many polar organisms consume so little oxygen that if a through-flow technique is used the flow must be kept at a low level and very carefully regulated. In this study a compromise was reached whereby water was allowed to flow through the experimental chambers overnight to allow the animals to acclimate to the experimental apparatus, and the flow was then sealed off for the measurement of oxygen consumption. This interrupted-flow technique was also compared with the simple sealed-chamber method.

Materials and Methods

Experiments were conducted with *Serolis cornuta* Studer and *Serolis polita* Pfeffer at −1.5, 0, +1.5, +3.0 and +4.5°C, about 20 animals of varying sizes of each species being used at each temperature. All animals were acclimated in aquaria at the experimental temperature for at least seven days and starved for the last 36 hours before the start of the experiment. This was found to be the time taken for the voiding of the majority of faeces from the digestive tract. Moulting or recently moulted animals were avoided as ecdysis is known to increase the metabolic rate (Bulnheim, 1974). The experiments were conducted in Perspex chambers submerged in a waterbath, which maintained the temperature in the chambers to an accuracy of ±0.1°C. The chambers used had a volume of about 170 ml for experiments with large *S. cornuta*, but 20-ml chambers were used for smaller individuals and for *S. polita*. The animals' own ventilatory movements were considered adequate to ensure water mixing. One animal was placed in each chamber and sea-water was allowed to flow through overnight (>12 hours) from a reservoir via a filter and a series of heat-exchanger coils. The water temperature in the reservoir was maintained at 0.5°C above the experimental temperature by a thermostatically controlled heater unit, to prevent oxygen super-saturation and consequent bubble formation in the tubing. The following day, when the animals were totally quiescent, the water flow was sealed off and the chambers were left undisturbed for periods ranging from 2 to 6 hours during which period the animals were observed to remain inactive. Replicate samples of water were then taken from each chamber for oxygen analysis. In each experiment there was a control chamber containing no animal, and the samples from this were used to calculate the 'initial' oxygen concentration. The change in oxygen concentration in the control chamber over the period of the experiment was found to be zero within the limits of experimental error.

Samples of water were collected in plastic syringes whose 'dead space' had previously been filled with paraffin, great care being taken to exclude all air bubbles. Oxygen analysis was by a semi-micro Winkler technique (Drew and Robertson, 1974) after Priddle (1977). With the large chambers, four replicate 20-ml samples were taken, and with the small chambers, two 10-ml samples were analysed. The difference between replicates was small and the mean volume was used to calculate oxygen concentration. The duration of the experiments was arranged to give a depletion of about 5–10%. It was concluded that this amount of depletion did not affect the animals' oxygen consumption as no consistent difference was observed between depletions of 5 and 10% of the initial value. After the experiment each animal was rinsed, blotted, and weighed fresh before drying at 60°C and ignition at 500–550°C for dry and ash weight determination.

To assess the active metabolic rate of *S. cornuta*, resting metabolism was initially measured as before at 0°C, and then the chambers were refilled with water and a magnetic stirrer switched on. The paddle was moved around the bottom of the chamber to keep the animal in a more or less continuous state of activity for periods of 1–1.5 hours, after which the oxygen depletion was again measured.

In order to determine the effect of recent handling on the metabolic rate of *S. cornuta* in simple sealed-chamber respirometry, some animals were acclimated and starved as usual, but then were placed into chambers at −1.5°C which were sealed immediately without any period to allow the animal to settle down. Oxygen consumption was measured in the normal manner.

Results

Regression equations were calculated relating ln (oxygen consumption) to ln (weight) at each experimental temperature and the relationships for dry weight are quoted in Table I and plotted in Fig. 1. The relationships for fresh and ash-free dry weight gave similar regression coefficients, and so are not quoted. Analyses of variance were performed for each species, and the intercepts of all lines were significantly different ($P < 0.001$). For *S. polita* the slopes of all lines were not significantly different ($P = 0.80$), but for *S. cornuta* there was only a difference between slopes ($P = 0.003$) if the line for +1.5°C was included. The slopes of the remaining four lines were not significantly different ($P = 0.85$).

Since these results demonstrated (as expected) that oxygen consumption varied with both temperature and size, a multiple linear regression relating ln (oxygen consumption) to both ln (dry weight) and temperature was calculated for each species, and the Q_{10} extrapolated from these equations (Table II). Analysis of variance shows that the planes defined by these equations are not parallel ($P < 0.001$), the partial regression coefficients for both weight and temperature being different ($P < 0.001$).

Both resting and active rates of oxygen consumption were measured in 16 *S. cornuta* ranging from 472 to 1095 mg in dry weight. With only one exception the active oxygen consumption was greater than the resting rate, the mean ratio of active/resting being 2.42 (standard deviation 0.84), and the maximum being 3.60.

Table I. Parameters of the regression equations, ln (oxygen consumption in $mm^3\ h^{-1}$) = $k \times$ ln (dry weight in mg) + ln a, for *Serolis cornuta* and *Serolis polita* at different temperatures.

Temp. (°C)	*k*	*s.e.k.*	*ln a*	r^2	*F*	*n*
Serolis cornuta						
−1.5	0.7212	0.2355	−1.3581	0.7865	77.366	23
0.0	0.8232	0.1866	−1.8757	0.8900	161.835	22
+1.5	0.9762	0.2256	−2.4623	0.9524	640.293	34
+3.0	0.7852	0.2003	−1.1409	0.9554	449.451	23
+4.5	0.8147	0.2364	−1.1364	0.7477	53.354	20
Serolis polita						
−1.5	0.6488	0.1572	−1.3013	0.7362	50.241	20
0.0	0.5812	0.2503	−0.8814	0.4487	17.902	24
+1.5	0.7581	0.1719	−1.4796	0.7329	65.847	26
+3.0	0.6667	0.1914	−0.9978	0.4949	18.618	21
+4.5	0.6054	0.2175	−0.7473	0.4763	14.553	18

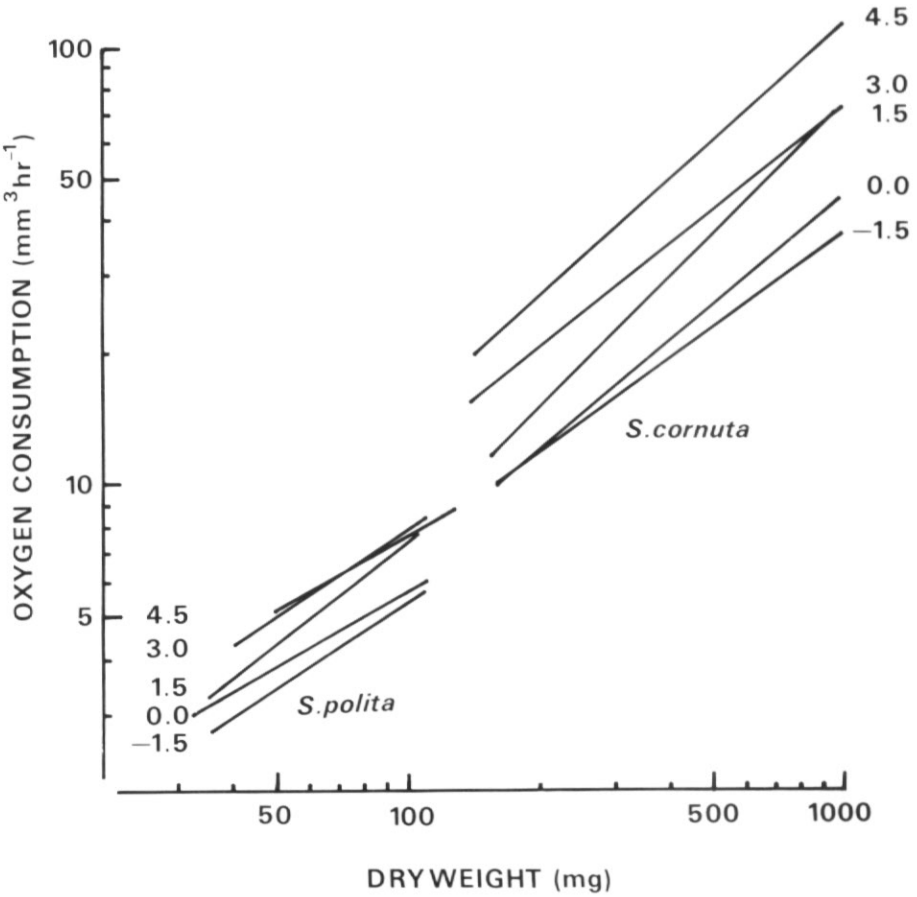

Fig. 1. Relationships (least squares regression lines fitted to logarithmically transformed data) between oxygen consumption and dry weight for *Serolis polita* and *Serolis cornuta* at different temperatures. Note logarithmic scales.

Table II. Parameters of the multiple linear regression equations, ln (oxygen consumption in mm^3 h^{-1}) = b_1 × ln (dry weight in mg) + b_2 × (temperature °C) + c, for *Serolis cornuta* and *Serolis polita*.

	S. cornuta	*S. polita*
b_1	0.8475	0.6449
Standard error of b_1	0.0242	0.0542
b_2	0.1437	0.0692
Standard error of b_2	0.0107	0.0095
c	−1.9607	+1.1619
r^2	0.9162	0.6559
F	662.82	103.92
n	122	109
Q_{10}	4.21	2.00

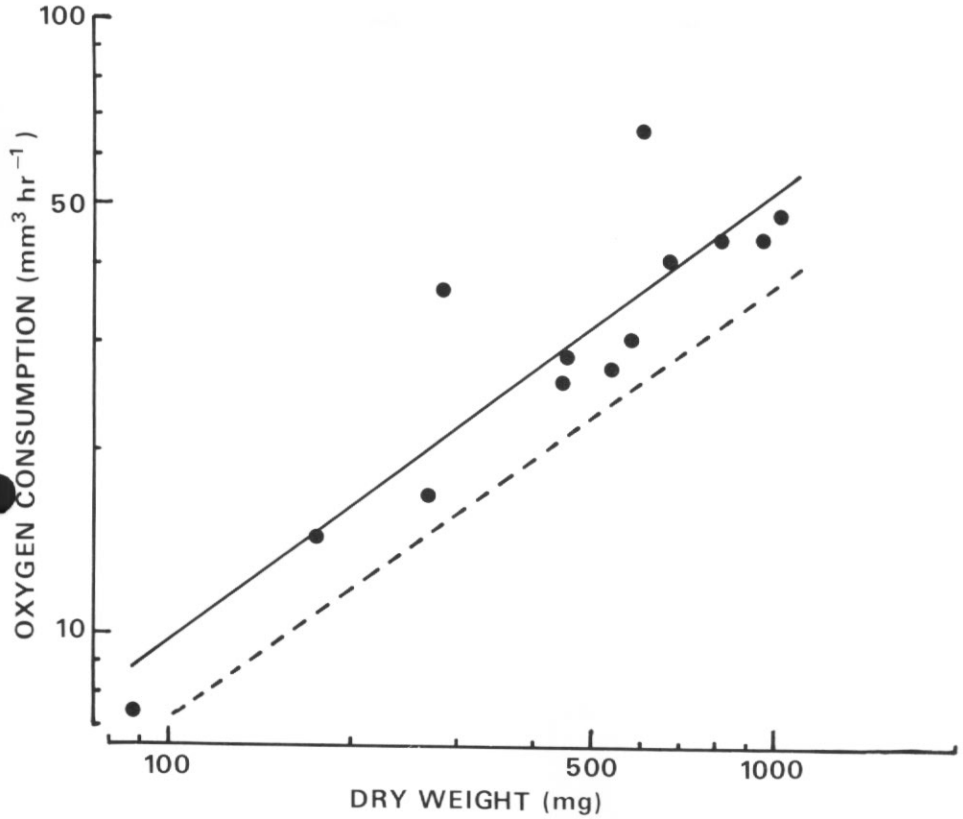

Fig. 2. The respiration rate of 13 *Serolis cornuta* at −1.5°C determined by simple sealed-chamber respirometry with a fitted least squares regression line (solid line). The dashed line shows the respiration rate at the same temperature predicted by the interrupted-flow technique. Note logarithmic scales.

The respiratory rates of 13 *S. cornuta* at −1.5°C as measured by simple sealed-chamber techniques are shown in Fig. 2 together with their fitted regression line. The regression line for the interrupted flow technique at −1.5°C, in which the animals are allowed to acclimate to the respirometer, is also plotted. The slopes of the relationship between oxygen consumption and dry weight are not significantly different ($P \gg 0.1$), but there is a difference between intercepts ($P = 0.028$) showing that the interrupted flow technique gave a significantly lower estimate of resting metabolic rate.

Discussion

Early studies of the respiratory rates of polar ectotherms suggested that they had higher oxygen consumptions than might be expected from the extrapolation to polar temperatures of respiratory data for temperate-water organisms (for review, see Clarke, 1983). Holeton (1973, 1974) demonstrated the importance of experimental protocol by showing that the oxygen consumption of polar fish was considerably lower than had previously been measured. This he attributed to having avoided

Table III. The respiration rate of several species of isopod at different temperatures expressed as the constants a and k in the equation $R = aW^k$, where R is the oxygen consumption in $mm^3\ h^{-1}$, and W is the dry weight in mg. Specific metabolic rate (a') calculated as $a\overline{W}^{(k-0.75)}$ where $\overline{W}$ is the geometric mean or median weight. Where necessary dry weight was calculated from ash-free dry weight using the appropriate conversion factors.

Species	*t(°C)*	*a*	*k*	*DW range*	$\overline{W}$	*a'*	*Source*
1. *Cirolana hardfordi*	12–13	0.809	0.67	0.4–114	6.8	0.69	Johnson, 1976
2. *Cirolana imposita*	10.4	0.407	0.67	0.8–30	4.9	0.36	Shafir and Field, 1980
	11.2	0.442	0.66	0.6–27	4.0	0.39	
	13.3	0.798	0.49	0.4–27	3.3	0.59	
	12.9	1.103	0.46	0.4–27	3.3	0.78	
	15.0	1.409	0.45	0.3–21	2.5	1.07	
3. *Cymodoce acuta*	20	2.530	0.70	0.19–154.8	4.5	2.35	Strelnikova, 1971
4. *Glyptonotus antarcticus*	−1.5	0.763	0.774	18–15540	530	0.89	White, 1975
	0.5	0.769	0.797	18–15540	530	1.03	
	2.5	0.934	0.798	18–15540	530	1.26	
	4.5	1.076	0.787	18–15540	530	1.36	
5. *Idotea baltica*	5	0.628	0.64	1–38	6.2	0.51	Bulnheim, 1974
	10	0.784	0.68	1.3–38	7.0	0.68	
	15	1.196	0.69	1.7–48	5.8	1.08	
	20	2.009	0.63	2.5–120	4.7	1.67	
6. *Idotea baltica*	4	0.680	0.683	10–100	32	0.54	Strong and Daborn, 1980
	6	0.686	0.729	10–100	32	0.64	
	9	0.591	0.840	10–100	32	0.81	
	11	0.485	0.923	10–100	32	0.88	
	14	0.465	0.998	10–100	32	1.10	
	16	0.488	1.143	10–100	32	1.91	
7. *Idotea baltica basteri*	20	2.206	0.79	0.03–82	1.6	2.25	Khmeleva, 1973
	25	4.889	0.85	0.03–30	0.9	4.84	

8. *Idotea metallica*	20	3.715	0.744	1–62	7.9	3.67	Ivleva, 1980
	25	4.855	0.664	0.5–62	5.6	4.05	
9. *Idotea ochotensis*	20	2.673	0.85	0.08–114	3.0	2.98	Strelnikova, 1971
10. *Mesidotea entomon*	10	0.251	0.85	60–1085	266	1.61	Babula and others, 1978
11. *Serolis cornuta*	−1.5	0.257	0.721	162–1372	555.5	0.21	This study
	0.0	0.153	0.823	150–1190	518.6	0.24	
	1.5	0.085	0.976	52–1843	328.3	0.31	
	3.0	0.320	0.785	45–1105	280.5	0.39	
	4.5	0.321	0.815	153–1239	546.2	0.48	
12. *Serolis polita*	−1.5	0.272	0.649	35–107	68.9	0.18	This study
	0.0	0.414	0.571	31–106	61.3	0.20	
	1.5	0.228	0.758	36–114	60.3	0.24	
	3.0	0.369	0.667	40–106	69.8	0.26	
	4.5	0.474	0.605	42–129	70.8	0.26	
13. *Sphaeroma hookeri*	5	0.418	0.71	?	5	0.39	Frier, 1976
	10	0.709	0.71	?	5	0.66	
	15	1.205	0.71	?	5	1.13	
	20	1.701	0.71	?	5	1.59	
14. *Sphaeroma rugicauda*	5	0.404	0.71	?	5	0.38	Frier, 1976
	10	0.574	0.71	?	5	0.54	
	15	0.900	0.71	?	5	0.84	
	20	1.276	0.71	?	5	1.20	
15 *Sphaeroma serratum*	9–11	0.625	0.688	5–25	11.0	0.54	Ivleva, 1977
	20	1.504	0.757	0.07–28	1.3	1.51	

subjecting the experimental animals to stress. More recent studies of Antarctic marine invertebrates have indicated that they too have low oxygen consumptions (White, 1975; Ralph and Maxwell, 1977; Houlihan and Allan, 1982). Accordingly it was decided to investigate the response of serolids and see if experimental protocol could affect the measured oxygen consumption in a similar way. Fig. 2 shows that the interrupted flow technique gave a significantly lower estimate of oxygen consumption than the simple sealed-chamber method, indicating that the former technique is preferable for estimating the basal metabolic rate.

The relationship between oxygen consumption (R) and weight (W) is frequently expressed as a power function:

$$R = aW^k.$$

The value of the exponent, k, has been reported to vary from 0.42 to 1.05 (Vernberg and Vernberg, 1970), but is usually in the range 0.6–0.8, and a general figure of 0.75 has been suggested (Hemmingsen, 1960).

Since oxygen consumption is markedly affected by temperature as well as weight, multiple linear regression analysis is a convenient way of quantifying the influence of both factors simultaneously. The parameters of the regression equations are given in Table II, the coefficient b_1 expressing the influence of weight on oxygen consumption, and b_2 the influence of temperature. The response of an organism to temperature is often measured in terms of its Q_{10} which is usually in the region of 2–3; Ivleva (1980) showed that the mean Q_{10} for aquatic crustacea in the range 0–5°C was 2.41. The Q_{10} of *Serolis*, calculated from the partial regression coefficient b_2, was found to be 2.00 for *S. polita* and 4.21 for *S. cornuta*. *S. polita* has a shallower bathymetric distribution than *S. cornuta* and, as short-term temperature fluctuations tend to be greater in shallow water, its lower Q_{10} may be an adaptation to stabilize its metabolic rate.

Attempts to compare physiological data from the literature of different species of marine isopod are fraught with the problem of finding enough results that are expressed in a sufficiently similar way to permit comparison. Although multiple linear regression would seem to be a promising technique for comparing respiratory data, it has seldom been calculated in practice, and consequently less accurate methods must be used for comparisons with results in earlier literature.

As a first step it is necessary to establish whether the relationship between weight and oxygen consumption in different species is sufficiently similar to permit any comparison at all. Data for 15 species of marine isopod at a variety of temperatures are given in Table III. In all cases the oxygen consumption (R, in $mm^3\ h^{-1}$) was expressed as a function of dry weight (W, in mg) using the equation:

$$R = aW^k$$

The quoted regression equations of six species at 4–5°C are plotted in Fig. 3. The slopes of all the lines are similar, and a common line fitted by eye has a slope of 0.75 in accordance with Hemmingsen's (1960) findings. In order to compare their relative metabolic rates it is necessary to compare the vertical displacement of each line from the common line. Assuming that the slopes of all the lines are the same, an estimate of the vertical displacement of any line is given by the intercept, $\ln a$, in the equation:

$$\ln R = k \ln W + \ln a,$$

where a is the metabolic rate of an animal of unit weight. By this means it is possible to compare the respiratory rates not only of different sized organisms, but also at different temperatures.

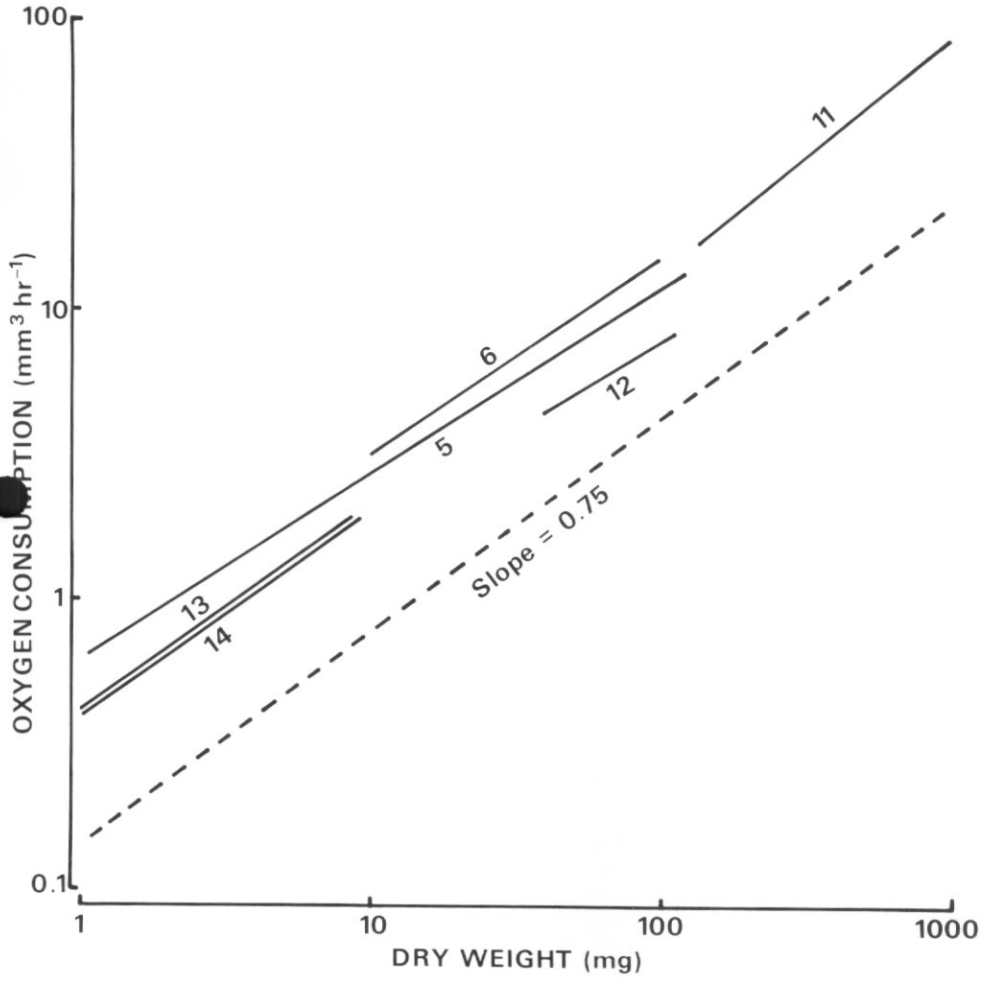

Fig. 3. Relationship between oxygen consumption and dry weight for several species of isopod at 4–5°C. Numbers refer to the species and data given in Table III. The dashed line represents a common slope (k) of 0.75, and is displaced vertically for clarity. Note logarithmic scales.

The major limitation of this method is that if the average weight of animals used in the experiments is not close to 1 mg, as was the case with *S. cornuta*, the value of the intercept, ln a, is a gross extrapolation from the experimental data and is markedly affected by small variations in the slope, k. Thus although the level of the graph for *S. cornuta* in Fig. 3 is higher than that for *S. polita*, it has a lower intercept due to its greater slope (Table I).

An alternative approach, which overcomes this problem, is to assume a common slope of 0.75 and recalculate a new intercept, a', on this basis from the equation:

$$a' = a\overline{W}^{k-0.75}$$

where $\overline{W}$ is the geometric mean or median weight determined from the weight range of the experimental data. This parameter may be termed 'specific metabolic rate' and is equivalent to the measure of 'oxygen consumption per metabolic body weight'

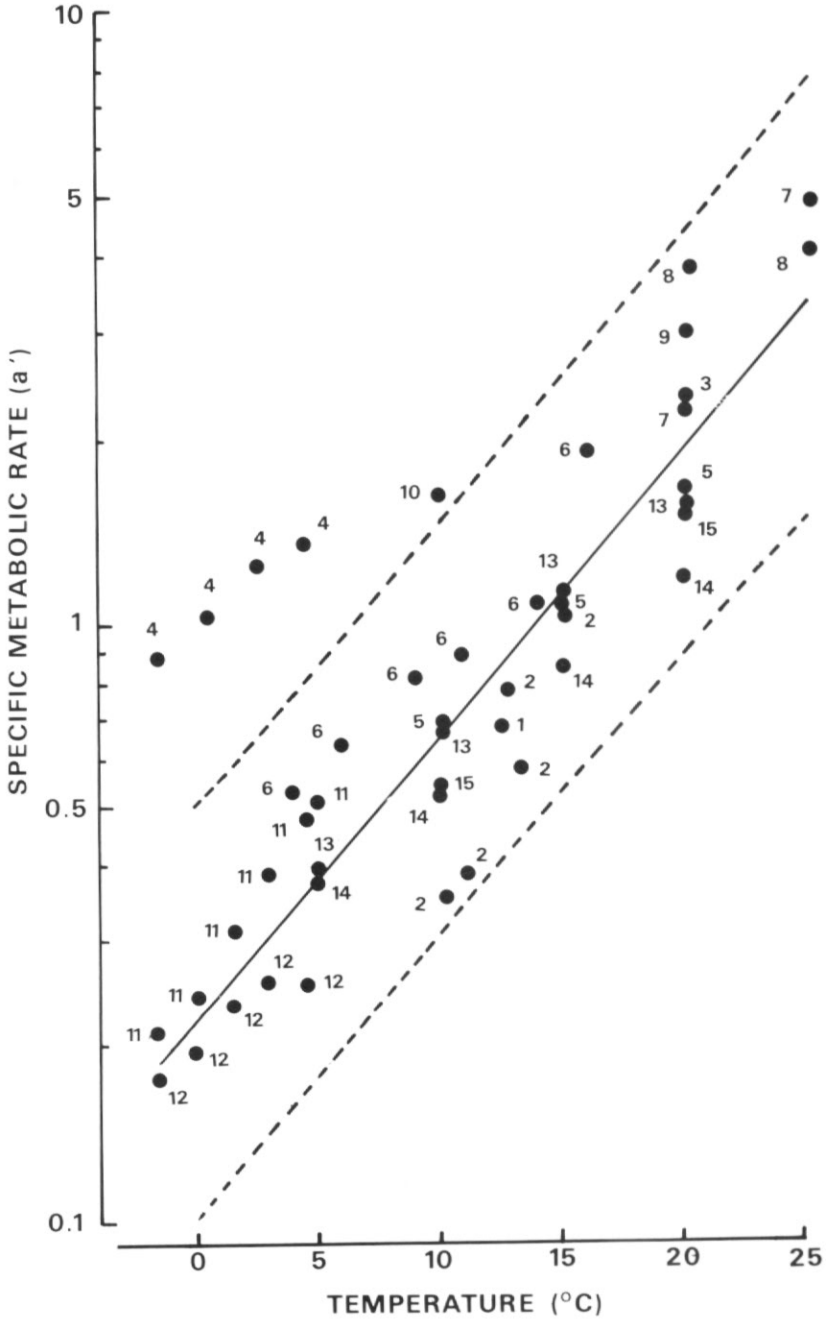

Fig. 4. Specific metabolic rates (a' in $mm^3\ h^{-1}$ of oxygen, see text) of several species of isopod in relation to temperature; numbers refer to the data in Table III; dashed lines are 95% confidence limits about fitted regression line. Note logarithmic vertical axis.

suggested by Kleiber (1965). Values of a' were calculated for all the data in Table III and are given in the penultimate column.

Both a and a' are clearly related to temperature (t) and regression equations expressing this relationship were calculated (excluding the data for *Glyptonotus antarcticus* and *Mesidothea entomon*, see below) as:

$$\ln a = 0.1068t - 1.4829$$
$$(n = 42;\ r^2 = 0.795;\ F_{1,41} = 155.20)$$

and:

$$\ln a' = 0.1090t - 1.5034$$
$$(n = 42;\ r^2 = 0.882;\ F_{1,41} = 189.43).$$

There is not much difference between the two equations, but the use of a' clearly reduces the variation. Moreover, for the larger species in Table III, a' seems to be more closely related to temperature than does a, and was therefore chosen for interspecific comparisons.

Values of specific metabolic rate (a') are plotted on a log scale against temperature in Fig. 4, together with the fitted regression line and 95% confidence limits. One of the most obvious features of the graph is that the majority of these marine isopods conform to a general relationship of increasing metabolic rate with temperature. The Q_{10} can be calculated from the slope of the regression equation to be:

$$\exp(10 \times 0.1090) = 2.97.$$

It is also possible to predict the metabolic rate of a 1-mg isopod at 0°C from the expression:

$$\exp(-1.5034 \pm 0.7939) = 0.22\ (0.10\text{–}0.49)\ (95\%\ \text{confidence limits}).$$

Ivleva (1980) reviewed the respiratory data for a wide variety of crustacea using a similar technique, and the metabolic rate that she suggested for 1-mg isopod at 0°C is very similar to that shown by this analysis (Table IV). She further showed that there were marked differences in the respiratory rates of different classes of Crustacea, with isopods and ostracods amongst the lowest. This can be attributed to their having a low level of activity, associated with benthic existence, and a high proportion of metabolically inactive cuticular tissue. Actively swimming crustaceans such as natantian decapods and mysids had higher levels of metabolism (Table IV). This means that when sensitive comparisons are made it is necessary to restrict all observations to a group of closely related organisms of similar ecology, in order to reduce the scatter of results. Even when this is done, within a homogeneous group such as the isopods, and when great care is taken with the comparative techniques, the variation is such that the metabolic rate must be elevated or depressed by a factor of at least 2.2 before it is statistically demonstrable.

Table IV. Values of '*a*' from Ivleva (1980) for different groups of crustaceans.

Euphausiids	0.65
Natantians and mysids	0.94
Amphipods	0.74
Isopods	0.26
Reptantians	0.59
Copepods	0.50

The specific metabolic rates of *Glyptonotus antarcticus* and *Mesidotea entomon* clearly lie above the line for other isopods (Fig. 4). Both species are very similar in shape and are atypical of other isopods: they are abnormally large (up to 170 mm for *G. antarcticus*, White, British Antarctic Survey, unpublished records; and 78 mm for *M. entomon*, Haahtela, 1978), and show little of the dorso-ventral flattening which is so characteristic of other members of the Order. In appearance and habits they are therefore more like reptantian decapods; their proportion of metabolically active tissue to cuticle is similar, and while their respiration rate is higher than other isopods it is comparable to that of the decapods. This underlines again the difficulties of comparing the metabolic rates of different types of organisms.

The concept of 'cold adaptation' (Scholander and others, 1953; Wohlschlag, 1964) whereby polar ectotherms were said to exhibit elevated metabolic rates, has been questioned on the theoretical grounds, and is not supported by more recent experimental evidence (Ivleva, 1973; Holeton, 1974; White, 1975; Clarke, 1980). The present analysis and that of Ivleva (1980) clearly show that metabolism in Crustacea is a function of temperature, and thus obeys the predictions of the Arrhenius equation. Furthermore, there is no reduction of Q_{10} as would be found if metabolism were elevated at lower temperatures.

This paper therefore highlights two problems of comparing the metabolic rates of different organisms. The first is that of finding a reliable and repeatable estimate of the metabolic rate, which necessitates very careful control over the experimental conditions and technique. The second is that of finding a satisfactory mathematical technique for comparing the data when both temperature and body size may differ widely in other studies. Different methods can lead to contrasting conclusions being drawn from the same set of data and compound the difficulties of experimental variation.

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