THE OXYGEN CONSUMPTION OF THE ANTARCTIC LAMELLIBRANCH *Gaimardia trapesina trapesina* IN RELATION TO COLD ADAPTATION IN POLAR INVERTEBRATES

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ABSTRACT. The oxygen consumption of the lamellibranch *Gaimardia trapesina trapesina* (Lamarck, 1819, p. 114) has been measured at different temperatures. At the temperature closest to the average environmental temperature, 0° C, the oxygen consumption of a 100 mg. tissue dry weight individual was 37·8 μg. O_2/hr. This value is comparable to the oxygen consumption of temperate lamellibranchs of the same body weight measured at temperatures close to 0° C and shows no "cold adaptation". Over the temperature range 0° to 5° C *Gaimardia trapesina trapesina* has a Q_{10} of approximately 2, indicating no regulation of its oxygen consumption with respect to temperature.

THE lamellibranch family Gaimardiidae is a cold-temperate family of molluscs, widely distributed in the sub-Antarctic (Dell, 1972). *Gaimardia trapesina trapesina* has been recorded from the Magellan region, the Falkland Islands, Marion Island, Iles Kerguelen, Iles Crozet and South Georgia (Dell, 1964). Another member of the family, *Kidderia bicolor*, is also found at South Georgia and some aspects of its biology there have been described by Ralph and Everson (1972). *G. t. trapesina* is very common on the fronds and stems of the giant kelp *Macrocystis pyrifera* that grows in sheltered bays around South Georgia.

There is very little information on the levels of oxygen consumption of Antarctic marine invertebrates (Armitage, 1962; Belman, 1973; Ralph and Maxwell, 1977). The oxygen consumption of *G. t. trapesina* is of special interest as it is one of the few sub-littoral organisms that is present on both sides of the Antarctic Convergence. It would appear to be a relatively recent addition to the Antarctic molluscan fauna. This paper presents information on the oxygen consumption of *G. t. trapesina* measured at different temperatures.

MATERIAL AND METHODS

All of the measurements of oxygen consumption were carried out during the southern summer of 1973-74 at King Edward Point, South Georgia. The animals were collected from *Macrocystis pyrifera* plants a few hundred metres from the laboratory. It was so easy and convenient to collect large numbers of animals in this way that they were not kept in the laboratory for long periods but were used a day or two after collection. The water temperature where the animals were collected was approximately 2° C.

The rates of oxygen consumption were measured by the method described by Ralph and Maxwell (1977); briefly, this was a closed bottle Winkler technique using screw-capped glass bottles of approximately 135 ml. capacity. Individual animals were placed in each bottle and each experiment lasted 1 hr. When removed from a kelp plant and placed in a bucket or other container, *G. t. trapesina* rapidly produces new byssus threads and attaches to the side or bottom of the container. Experiments were carried out at three temperatures: 0°, 5° and 7° C. Animals were kept at the experimental temperature for 12–18 hr. before their oxygen consumption was measured. Survival in the laboratory was good at the two lower temperatures but there was some mortality at the highest temperature. The animals used in experiments were in good condition as far as it was possible to assess.

At the end of each experiment the shell lengths of the animals were measured and the soft tissues were dissected away from the shells, dried at 60° C and weighed. Oxygen consumption was calculated as μg. O_2/animal/hr.

RESULTS

The results of the oxygen-consumption measurements are shown in Fig. 1 at the three experimental temperatures. The oxygen consumption is plotted against tissue dry weight (mg.) on logarithmic scales. Oxygen consumption (Y) and body weight (X) are related by the ex-

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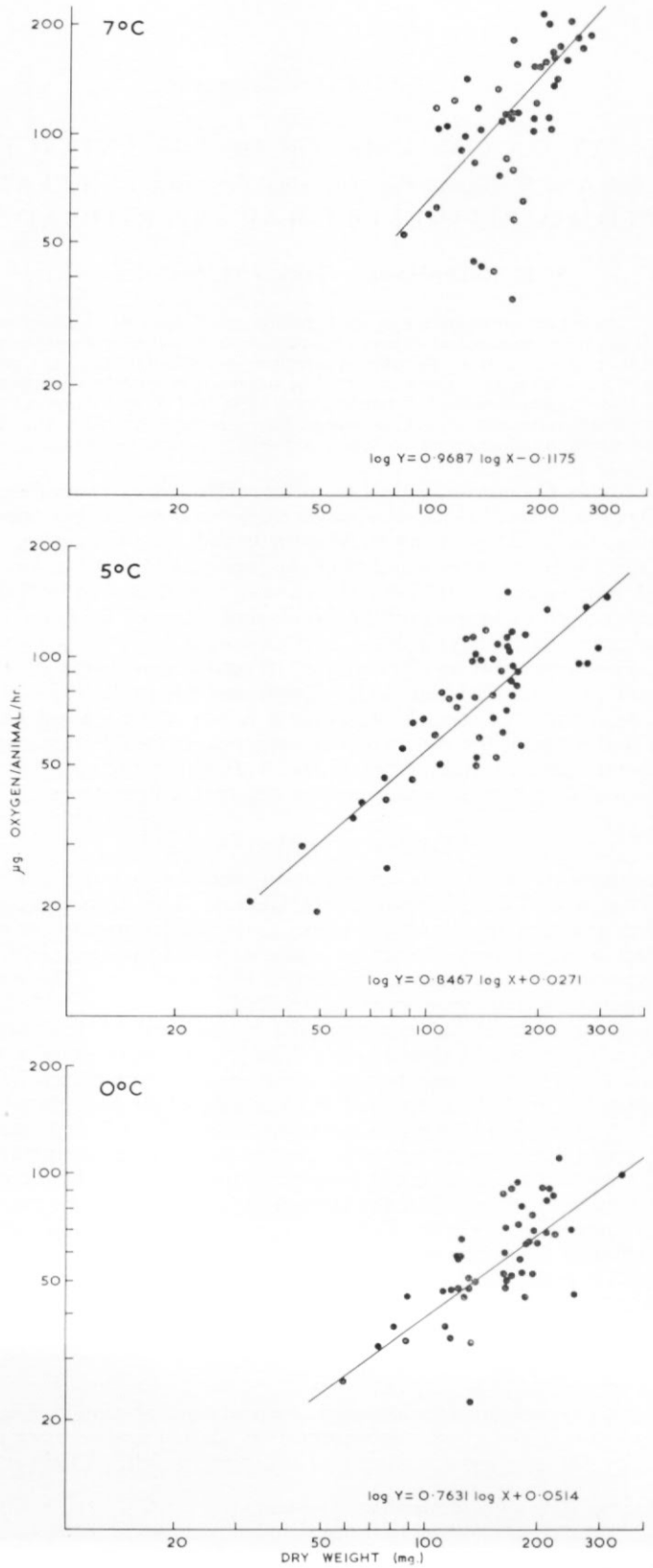

Fig. 1. The oxygen consumption of *Gaimardia trapesina trapesina* at 0°, 5° and 7° C. The regression lines are the actual lines and do not use the calculated common regression coefficient.

pression $Y=aX^b$ (Zeuthen, 1947; Prosser and Brown, 1961) which is more usually expressed as

$$\log Y = b \log X + \log a.$$

The regression equations for *G. t. trapesina* at the three temperatures are:

0° C $\log Y = 0{\cdot}7631 \log X + 0{\cdot}0514$,
5° C $\log Y = 0{\cdot}8467 \log X + 0{\cdot}0271$,
7° C $\log Y = 0{\cdot}9687 \log X - 0{\cdot}1175$.

At all three temperatures the correlation between oxgen consumption and body weight is highly significant ($p<0{\cdot}001$). The three regression coefficients are not significantly different from each other and a common regression coefficient has been calculated. Its value is 0·8463 and the re-calculated regression lines using this figure are:

0° C $\log Y = 0{\cdot}8463 \log X - 0{\cdot}1325$,
5° C $\log Y = 0{\cdot}8463 \log X + 0{\cdot}0279$,
7° C $\log Y = 0{\cdot}8463 \log X + 0{\cdot}1554$.

Although the slopes of the lines are not significantly different, the intercepts of the three lines are significantly different from each other ($p < 0{\cdot}001$).

The oxygen consumption of three weights of animal, 50, 100 and 200 mg. has been calculated for each temperature and are given in Table I.

TABLE I. OXYGEN CONSUMPTION OF *Gaimardia trapesina trapesina* (μg. O_2/animal/hr.)

Temperature	*Weight* (mg.) 50	100	200
0° C	20·2	36·3	65·3
5° C	29·2	52·5	94·5
7° C	39·2	70·4	126·7

Values of Q_{10} have been calculated for each temperature interval and are shown in Table II.

TABLE II. Q_{10} OF OXYGEN CONSUMPTION OF *Gaimardia trapesina trapesina*

Temperature interval	Q_{10}
0–5° C	2·09
0–7° C	2·57
5–7° C	4·33

DISCUSSION

As already pointed out, the b values (regression coefficients) determining the relationship between oxygen consumption and body weight in *G. t. trapesina* are not significantly different from each other at the three experimental temperatures. Hemmingsen (1960) has suggested that a b value of 0·75 might be taken to apply to poikilotherms in general and for lamellibranchs in particular; Ansell (1973) quoted a mean value of 0·703 for 16 species from the west coast of Scotland. The b values recorded here for *G. t. trapesina* are in broad agreement.

The oxygen-consumption rates of Antarctic invertebrates are of interest because of the information they may provide regarding the concept of cold adaptation. The suggestion has grown in the literature that polar poikilotherms have a much higher resting or standard metabolism at their environmental temperatures than have tropical or temperate poikilotherms, when the metabolic rates of the latter are either measured at polar temperatures or

extrapolated to low temperatures from measurements made at their own higher environmental temperatures. This elevated metabolic rate is generally referred to as cold adaptation. There is a great deal of experimental evidence for this, the most often quoted coming from Scholander and others (1953), Bullock (1955), Wohlschlag (1960, 1964) and Brett (1970). However, the concept of cold adaptation has been criticized on two grounds. First, it is difficult to see what advantage a high resting or standard metabolic rate confers on an animal living at a low temperature in an environment where production is low, as in the Arctic, or extremely seasonal as in the Antarctic. This point has been discussed by Dunbar (1968) and Holeton (1973). Secondly, much of the concept is based on work done on fish, especially Antarctic fish (Wohlschlag, 1960, 1964). It is known that measurements of oxygen-consumption rates of fish are profoundly influenced by the experimental techniques used; handling of fish or manipulating them into a respiration chamber may produce an oxygen debt that can elevate the respiration rate for many hours, although the fish is apparently quiescent. Holeton (1974) has measured the respiration rates of a number of Arctic fish species after several days in respiration chambers. They were found to have low rates of oxygen uptake after acclimation and he did not feel they could be considered to exhibit "cold adaptation".

A problem exists in trying to compare the respiration rates of animals from different latitudes and different temperature regimes. Many polar and tropical forms are stenothermal and it is impossible to measure their respiration rates at temperatures away from their normal environmental levels. In extrapolating respiration rates of tropical and temperate animals to polar temperatures, many authors have used Krogh's (1916) standard line of metabolism. Holeton (1974) pointed out, as indeed Krogh himself did, that at the low-temperature end this line is based on a very small amount of experimental work and its use is probably not justified. Taking this and the question of experimental technique into account, Holeton (1974) concluded that the concept of cold adaptation in polar fish is not a viable one.

The situation in polar invertebrates is just as open to question. The conclusions drawn by Scholander and others (1953), regarding cold adaptation in a number of Arctic invertebrates, depend upon extrapolation of results for tropical forms using Krogh's (1916) line and may be criticized on that ground. Thorson (1936) claimed that a number of Arctic lamellibranchs show cold adaptation when compared with similar species from the tropics and temperate regions. However, he quoted his results as ml. O_2/unit weight of animal/hr. without giving the weights of his experimental animals. Although Thorson may have been right in his conclusions, it is not possible to compare his results with any others because of this lack of information. Some other examples of possible cold adaptation in northern forms have been given by Dunbar (1968).

There is very little information on the levels of oxygen consumption in Antarctic invertebrates. Armitage (1962) measured the oxygen consumption of the amphipod *Orchomonella chilensis* from McMurdo Sound. He used a range of temperatures from $-1{\cdot}8°$ to 12° C, although survival was poor at the highest temperature. Armitage claimed that *O. chilensis* is cold adapted with respect to temperate amphipods by extrapolation upwards from the rise in its oxygen consumption over the temperature range from 8° to 10° C. In fact, over the more realistic temperature interval from $-1{\cdot}8°$ to 4° C there was very little increase in oxygen consumption and, if this part of the respiration–temperature curve is extrapolated, *Orchomonella chilensis* cannot be considered to be cold adapted.

McWhinnie (1964) has worked on Antarctic krill *Euphausia superba* and suggested that it shows cold adaptation as its oxygen consumption at 0° C is higher than at 1° C. Although detailed comparisons are not possible because McWhinnie does not provide exact weight information, her results for *E. superba* are broadly comparable with the respiration rate of *Euphausia pacifica* at 10° C (Lasker, 1966), indicating that *E. superba* is probably cold adapted.

It has been clearly shown by White (1975) that the Antarctic isopod *Glyptonotus antarcticus* is not cold adapted and this is also the case for the Antarctic limpet *Nacella* (*Patinigera*) *concinna* (Ralph and Maxwell, 1977).

There are no measurements of oxygen consumption of other Antarctic lamellibranchs with which the results for *G. t. trapesina* may be compared. By contrast, there is a wealth of information available for temperate species. Two species for which oxygen-consumption rates have been measured at low temperatures are *Mytilus edulis* (Read, 1962) and *Cardium edule* (Newell

and Northcroft, 1967). These two are comparable with *G. t. trapesina* in terms of size and, although *C. edule* is an infaunal animal, there appears to be no evidence that the oxygen consumption of infaunal lamellibranchs is different from that of epifaunal ones. Table III provides values of the oxygen consumption of these two species taken from the sources mentioned above. Newell and Northcroft (1967) gave two regression lines for *C. edule* at each temperature, one corresponding to minimal activity, the other to a maximal level. The figure in Table III is a mean of these two levels.

TABLE III. THE OXYGEN CONSUMPTION OF *Cardium edule* AND *Mytilus edulis* (NEWELL AND NORTHCROFT, 1967; READ, 1962), IN μg./animal/hr.

Temperature	*Weight* (mg.) 50	100	200
	Cardium edule		
3° C	61·0	74·2	89·6
5° C	74·3	94·2	120·4
	Mytilus edulis		
3° C	30·6	51·4	86·4
7° C	68·3	103·8	157·6

When these values are compared with the rates obtained for *G. t. trapesina* (Table I), it is clear that *G. t. trapesina* shows no cold adaptation of its oxygen consumption.

The Q_{10} of 2·09 for *G. t. trapesina* over the temperature range of 0° to 5° C indicates that the species shows no metabolic independence of temperature over this range. The higher Q_{10} value of 4·33 seen between 5° and 7° C reflects the fact that the higher temperature is probably close to the upper thermal limit of the species at South Georgia. The increased scatter in the results at this temperature supports this. It is of interest that White (1975) obtained similar Q_{10} values for the non-cold adapted isopod *Glyptonotus*. In contrast, McWhinnie (1964) found a Q_{10} of 1·1 for *Euphausia superba* from 0° to 5° C, a species that may be considered cold adapted.

G. t. trapesina has presumably spread to South Georgia from the Falkland Islands, 1,330 km. away. It could easily be carried there on pieces of kelp; on sea passage from South Georgia to the Falkland Islands large pieces of floating kelp may be seen frequently. It would be valuable to have some information on the oxygen consumption of *G. t. trapesina* from the Falkland Islands and to compare the thermal tolerance of animals from the two areas.

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