

FACTORS AFFECTING OXYGEN CONSUMPTION IN THE SCALLOP *CHLAMYS DELICATULA* (HUTTON)

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ABSTRACT

The effect of body size, activity, feeding and declining PO_2 on the rate of oxygen consumption in the scallop *Chlamys delicatula* were investigated. Vigorous swimming activity led to a 2.4 fold increase in the rate of oxygen consumption. Feeding did not cause an increase in oxygen consumption. Neither activity nor feeding significantly affected the slope of the line relating log body weight to log oxygen consumption.

Oxygen consumption in declining ambient oxygen tension was studied. Use of the oxygen dependence index K_1/K_2 (Bayne 1971) suggests that *C. delicatula* is not a good oxyregulator. The relationship between the oxygen dependence index and body size is given by the exponential equation $K_1/K_2 = 115.78QO_2^{0.769}$ where QO_2 is the weight-specific oxygen consumption ($ml O_2 \cdot g^{-1} \cdot h^{-1}$).

INTRODUCTION

Although oxygen consumption in bivalve molluscs has been widely studied (Tang 1933, Kinne 1970, Thompson & Bayne 1972, Vahl 1973 a, Bayne & Scullard 1977, and Widdows 1978), there has been very little work done concerning the Pectinidae. Spärck (1936, cited by van Dam 1954) found that the resting metabolism of scallops and other bivalves capable of swimming was markedly higher than that of more sedentary species. Van Dam (1954), however, reported oxygen consumption rates for *Pecten grandis* Solander and *P. irradians* Lamarck which were within the range of values published for non-swimming boreal species. Vahl (1972, 1978) and McLusky (1973) reported oxygen consumption levels for *Chlamys opercularis* and *C. islandica* which were also within the range of published values for sedentary species (e.g. Bayne *et al.* 1976 for mussels), although the levels reported are in the lower part of the range.

Both activity and feeding are known to cause an increase in oxygen consumption in many species (Saunders 1963, Newell 1970, Wallace 1973, Crisp *et al.* 1978). Bayne & Scullard (1977) have used feeding as a measure of activity in the mussel *Mytilus edulis* (L.) and have described a 'specific dynamic action'

due to feeding. McLusky (1973) did not observe such a response to food in *Chlamys opercularis*. It was, therefore, of interest to investigate the rate of oxygen uptake in the deep water scallop *Chlamys delicatula* and to investigate the effects of both feeding and activity on oxygen uptake.

In preliminary experiments it was noticed that scallops survived periods of up to 12 hours anoxia and therefore the effect of declining oxygen tension on oxygen consumption was also investigated.

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MATERIALS AND METHODS

Specimens of *Chlamys delicatula* were dredged on the outer continental shelf east of the Otago Peninsula (approximate position 171°03'E 45°47'S) at a depth of about 135 m. The animals were held in shallow tanks in running seawater from Otago Harbour at 10-14 °C and 33.5 ‰ salinity. Scallops were starved for at least two weeks before use in experiments.

Oxygen consumption was measured using a Radiometer oxygen electrode connected via a Radiometer PHM 71 meter to a Smith's Servoscribe chart recorder. The experimental procedure has been described by Taylor & Brand (1975) and Crisp *et al.* (1978). All experiments were carried out at 10 °C between July 1978 and April 1979.

The effect of size on oxygen consumption was studied using animals in the size range 0.025-1.5 g dry weight. Small animals (dry weight < 0.015 g) were found to be extremely disturbed by the necessary handling and were therefore not used. Oxygen consumption was calculated using the formula given by Crisp *et al.* (1978) and expressed as $\text{ml} \cdot \text{h}^{-1} \cdot \text{animal}^{-1}$ (VO_2).

The relationship thus established was assumed to represent a 'routine' or 'resting' rate of oxygen consumption. To obtain an 'active' rate, scallops were induced to swim vigorously for one minute before being placed in the respiration chamber. In initial experiments an extract was prepared by grinding starfish (*Sclerasterias mollis*) tissue to a paste with seawater. The extract induced swimming in most scallops but frequently an animal would close its valves after swimming for a few seconds and remain closed for up to two hours. In subsequent experiments, however, continuous swimming could be maintained by repeated stimulation of the scallop mantle with a starfish foot.

A 'fed' rate was obtained by placing scallops in a suspension of algal cells (*Pavlova lutheri*) for one hour before placing them in the respiration chamber. The concentration of algal cells used was $30\,000 \text{ cells} \cdot \text{ml}^{-1}$ (Taylor & Brand 1975). The suspension was stirred continuously with an immersible magnetic

stirrer and the scallops appeared to be open and pumping normally. The concentration of the suspension was determined by measuring the absorbance at 520 nm in a Bausch & Lomb Spectronic 20 spectrophotometer and checked by direct counting. Nicholson (1978) found it necessary to condition *Pecten novaezelandiae* for one week to eating algae. However, the absorbance of the suspension decreased progressively during the course of the experiment and, since the suspension was stirred continuously, this decrease was attributed to feeding activity by the scallop.

The effect of declining oxygen tension on the oxygen uptake of *C. delicatula* was determined by allowing animals to deplete completely the oxygen supply in the respiration chamber (Taylor & Brand 1975, Shumway 1978). To minimize variations due to differences in weight between individuals, % air saturation was plotted against $VO_2/W^{0.539}$ where W is dry flesh weight in g and 0.539 is the exponent relating VO_2 to body weight in resting animals (Bayne & Livingstone 1977).

RESULTS

Effect of size, activity and feeding on oxygen consumption

Table 1 gives the linear regression equations relating dry tissue weight and oxygen consumption for 'resting', 'active' and 'fed' *Chlamys delicatula*. Oxygen consumption ($\text{ml O}_2 \text{ consumed} \cdot \text{h}^{-1}$) is given by the equation $Y = aX^b$ where Y = oxygen consumption ($\text{mg} \cdot \text{h}^{-1}$), X = tissue dry weight (g), b is the slope of a plot of log dry weight versus log oxygen consumption and a is a constant. In all cases $p < 0.001$ for the appropriate degrees of freedom.

TABLE 1. The relationship between body size and rate of oxygen consumption in 'resting', 'active' and 'fed' *Chlamys delicatula*.

	Number of observations (n)	Range of dry weights (g)	a	b	Correlation coefficient
'resting'	14	0.026-1.48	0.166	0.539	0.98
'active'	11	0.015-1.02	0.398	0.651	0.96
'fed'	20	0.011-0.815	0.147	0.527	0.94

The rate for 'active' animals is 2.4 times higher than the rate for 'resting' animals and 2.7 times higher than the rate for 'fed' animals. The slopes and intercepts of the three regression lines were tested for significant differences (Wilson 1975). There is no significant difference between the slopes, but the

TABLE 2. Comparisons of regressions of oxygen consumption ($\text{ml} \cdot \text{h}^{-1}$) on dry weight (g) for 'active', 'fed' and 'resting' *Chlamys delicatula*.

	Difference between intercepts. Variance ratio	p	Difference between slopes. Variance ratio	p
'active' vs 'fed'	36.6452	0.000001	1.9195	0.176852
'active' vs 'resting'	50.8930	0.000000	2.8416	0.106656
'fed' vs 'resting'	2.1946	0.148274	0.3990	0.532225

intercept for the 'active' line is significantly higher than the intercept for the 'resting' and 'fed' lines. The intercepts of the 'resting' and 'fed' lines are not significantly different (Table 2).

Effect of declining oxygen tension on oxygen consumption

The rate of oxygen consumption ($\text{VO}_2/\text{W}^{0.539}$) is plotted against % air saturation in Fig. 1. Bayne & Livingstone (1977) fitted three statistical models to data relating the rate of oxygen consumption to oxygen tension and found that for

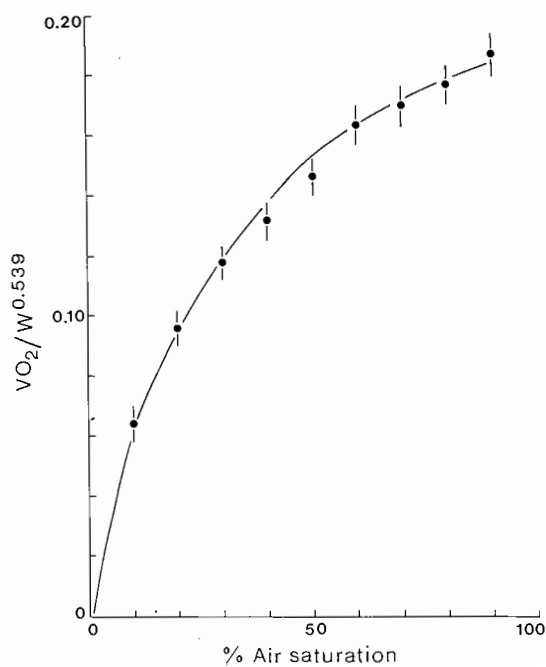


FIG. 1. Effect of declining oxygen tension on oxygen consumption.

non-standardised data the hyperbolic expression used by Tang (1933) and Bayne (1971) provided the best fit. This expression is given by:

$QO_2 = \frac{PO_2}{K_1 + K_2 \cdot PO_2}$, where QO_2 = weight specific oxygen consumption ($ml \cdot g^{-1} \cdot h^{-1}$), PO_2 = oxygen tension (mm Hg), K_1 and K_2 are the intercept and slope, respectively, of a plot of PO_2 against PO_2/QO_2 .

The ratio K_1/K_2 can then be used as an index of oxygen independence (Bayne 1971). As the ratio K_1/K_2 increases, the rate of oxygen consumption becomes more directly proportional to oxygen tension (oxygen dependence) and as the ratio K_1/K_2 decreases, the rate of oxygen consumption approaches a constant (oxygen independence).

TABLE 3. Some regression equations for K_1/K_2 , the 'oxygen-dependence index', against QO_2 , the weight specific oxygen consumption.

Species	Regression equation	Correlation coefficient	No. of determinations	Source
<i>Geloina ceylonica</i>	$K_1/K_2 = 3.88 QO_2^{0.457}$	0.626	10	Bayne 1973
<i>Anadora granosa</i>	$K_1/K_2 = 6.46 QO_2^{0.615}$	0.692	7	Bayne 1973
<i>Modiolus demissus</i>	$K_1/K_2 = 62.71 QO_2^{0.930}$	0.712	10	Shumway & Youngson, in press
<i>Mytilus edulis</i>	$K_1/K_2 = 75.50 QO_2^{0.818}$	0.648	10	Bayne 1978*
<i>Chlamys delicatula</i>	$K_1/K_2 = 115.78 QO_2^{0.769}$	0.815	6	present study
<i>Laevicardium crassum</i>	$K_1/K_2 = 550.00 QO_2^{1.829}$	0.847	10	Bayne 1971*
<i>Arctica islandica</i>	$K_1/K_2 = 1000.00 QO_2^{1.7}$		15	Taylor & Brand 1975**

* See Shumway & Youngson, in press.

** Equation estimated from Fig. 3 in Taylor & Brand (1975).

The relationship between the oxygen dependence index and the weight specific oxygen consumption is given by an exponential equation. This relationship is given in Table 3 for *Chlamys delicatula* and five other species of bivalves. The value of the constant in the regression equation is an indication of the degree of oxygen dependence exhibited by a species. For a *C. delicatula* with a QO_2 of 1, K_1/K_2 is 115.78. This is a relatively high value indicating that *Chlamys delicatula* is not a good oxyregulator.

DISCUSSION

The 'resting' rate of oxygen consumption in *C. delicatula* is in close agreement with those reported by Vahl (1972, 1978) for *C. opercularis* (O_2 consumption of about $0.098 ml \cdot h^{-1}$ for a 0.3 g dry weight animal acclimated for 75 days)

TABLE 4. Some relationships between oxygen consumption and body size in the Pectinidae. a and b are parameters in the equation $VO = aW^b$, where VO_2 = oxygen consumption ($\text{ml} \cdot \text{h}^{-1} \cdot \text{animal}^{-1}$) and W = dry tissue weight (g).

Species	Number tested (n)	Size range (g dry wt)	Temp. ($^{\circ}\text{C}$)	a	b	Source
<i>Chlamys islandica</i>	46	0.003-5.8108	2.2-7.7	0.141	0.78	Vahl 1978
<i>C. delicatula</i>	14	0.026-1.48	10	0.166	0.539	present study
<i>C. opercularis</i>	10	0.3 -3.0	10	0.385	0.63	McLusky 1973*
<i>Pecten grandis</i>	5	1.35 -3.45**	16-24	0.748	0.98	van Dam 1954

*Equation calculated from McLusky (1973, fig. 4).

** Assuming tissue water content of 85 %.

and for *C. islandica* (Table 4), although Vahl reports a much lower oxygen consumption for small *C. islandica*. It is possible that in our present experiments smaller individuals of *C. delicatula* show an abnormally high oxygen consumption due to disturbance during handling, although many factors can affect the rate of oxygen uptake (Zeuthen 1947, Hemmingsen 1960, Widdows 1978). Although McLusky (1973) reported an apparently higher rate for *Chlamys opercularis* than that given by Vahl (1972), inspection of the data suggests that there is no difference between the figures reported by McLusky ($0.12 \text{ ml O}_2 \cdot \text{h}^{-1}$ for a 0.3 g animal acclimated for seven weeks) and Vahl (see figures cited above). If there is a real difference, this may in part reflect a seasonal variation for *C. islandica* and the phenomenon has also been described by Bayne & Scullard (1978) (*Thais lapillus* L.) and by Widdows (1978) (*Mytilus edulis* L.). Both authors found a marked increase in oxygen consumption in the summer. Widdows (1978) points out that this seasonal variation is probably a response to the gametogenic cycle rather than a direct response to temperature. De Vooy (1976) also found variations in the oxygen uptake of *Mytilus edulis* which were related to reproduction. No account was taken of seasonal variation in our study although there was no obvious elevation of oxygen uptake in animals tested during the summer months.

Vahl (1978) also found that only an insignificant part of the seasonal variation in oxygen consumption of *C. islandica* could be explained by seasonal temperature variations. He did show, however, that a significant part of the variation could be accounted for by the amount of particulate matter in the water masses from which the scallops were collected and suggested that part of the increase in oxygen consumption was due to the 'specific dynamic action of food' (Bayne & Scullard 1977). McLusky (1973) found that the addition of food during an experiment did not increase oxygen consumption in *C. opercularis* and our results also suggest that there is no 'specific dynamic action of

food' in *C. delicatula*. This may be at least partly explained by looking at the feeding behaviour of the scallop. *C. delicatula* is sublittoral and probably feeds continuously, whereas *Mytilus edulis* is not strictly a continuous feeder and is therefore adapted to a discontinuous food supply (Thompson & Bayne 1972). Other species in which an elevated oxygen uptake in response to feeding has been observed are also discontinuous feeders. Saunders (1963) found an immediate rise in the respiration rate of the Atlantic cod (*Gadus morhua* L.) and the rate remained high for several days. Crisp *et al.* (1978) found that the oxygen uptake of the carnivorous gastropod *Nassarius reticulatus* remains elevated for two to three days after feeding.

Although some individuals were observed to survive long periods of anoxia, *Chlamys delicatula* does not appear to be a good oxyregulator. There has been some discussion on the methods of treating data from experiments concerning oxygen uptake in response to declining ambient oxygen tension (Tang 1933, Bayne 1971, Mangum & van Winkle 1973, Bayne & Livingstone 1977, Shumway & Youngson, in press). The method used here was shown by Bayne & Livingstone (1977) to provide a good fit to non-standardised data.

The equation given in Table 3 relating K_1/K_2 to weight-specific oxygen consumption in *C. delicatula* fits the general pattern suggested by Bayne (1973), i.e. there is a general trend for increasing oxygen dependence with decreasing likelihood of encountering low environmental oxygen tension in the natural habitat. *Geloina ceylonica* and *Anadara granosa* both regularly experience low oxygen tension in their natural habitats (Bayne 1973). *Mytilus edulis* and *Modiolus demissus* are intertidal and may therefore be subjected to periods of hypoxia during shell closure. The value of the constant in the equation relating K_1/K_2 to QO_2 indicates that these species show less ability to regulate oxygen consumption than *Geloina* and *Anadara*. *C. delicatula*, *L. crassum* and *A. islandica* are all sublittoral species and show the least ability to regulate oxygen consumption. *C. delicatula* is unlikely to encounter low oxygen tension in its natural environment. The oxygen content, measured by the Winkler method, of the habitat water of *C. delicatula* was found to be $6.24 \text{ ml O}_2 \cdot \text{l}^{-1}$ in September 1978 and $5.65 \text{ ml O}_2 \cdot \text{l}^{-1}$ in February 1979. These values represent 98.3 % and 92.6 % saturation respectively.

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