

# OXYGEN CONSUMPTION IN SIX SPECIES OF CHITONS IN RELATION TO THEIR POSITION ON THE SHORE

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## ABSTRACT

Aerial and aquatic oxygen consumption rates have been measured in six species of intertidal chitons with respect to zonation, size and oxygen concentration of the external medium. Those species occurring highest on the shore were found to have a lower rate of aquatic oxygen consumption than those species occurring lowest on the shore, with mid-shore species showing intermediate rates. Aerial oxygen consumption rates were similar in most species and were not strictly correlated with their position on the shore. High shore chitons had higher or equal rates in air than in water, while low shore species had higher aquatic than aerial rates. It was also found that the six species could be grouped with respect to their oxyregulatory capabilities when exposed to declining oxygen tensions and these groups could be correlated with the species intertidal zonation: high shore species show a high degree of oxygen independence, mid-shore species a moderate degree and low shore animals little or no regulatory capabilities.

## INTRODUCTION

Animals living within the intertidal zone are subject to varying degrees of emersion or exposure to air depending on their shore height. The ability of intertidal animals to utilize oxygen in both air and water has been demonstrated by a number of workers (see Newell 1970). Numerous comparisons both interspecifically (e.g. Barnes *et al.* 1963, Micallef & Bannister 1967) and intraspecifically (e.g. Southward 1955, Barnes & Barnes 1959, Sandison 1966) have established that respiratory phenomena of organisms may be influenced by their height on the shore. Only Micallef & Bannister (1967) studied both aerial and aquatic respiration with respect to zonation.

The respiratory response of different species of bivalve molluscs to declining oxygen tension in relation to the possibility of experiencing hypoxia has been studied by Bayne (1973), and Taylor & Brand (1975 a, b). No such studies are known for chitons.

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Studies on chiton respiration are few (Nagabhushanam & Murti 1972, Peterson & Johansen 1973, Kincannon 1975, Robbins 1975) and none of these studies have correlated interspecific differences in aerial and aquatic respiration rates to the animals' intertidal location.

Six species of intertidal chitons are commonly found within the Otago Harbour, each at characteristically different varying heights on the shore, providing an ideal opportunity to examine aerial and aquatic respiration and the response to declining oxygen tension in relation to zonation.

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We wish to dedicate this paper to the late Dr. C.R. Boyden whose enthusiasm and interest in chitons stimulated the present investigation.

## MATERIAL AND METHODS

Specimens of *Cryptoconchus porosus* Burrow, 1815, *Acanthochitona zelandicus* (Quoy and Gaimard, 1835), *Onithochiton neglectus* Rochebrune, 1881, *Ischnochiton maorianus* Iredale, 1914, *Amaurochiton glaucus* (Gray, 1828) and *Sypharochiton pelliserpentis* (Quoy and Gaimard, 1835) were collected locally from the Otago Harbour, Portobello, New Zealand. As closely as possible, specimens of each species were collected from the upper-most range of their distribution zone on the shore. All animals were kept at 15 °C in aquaria supplied with running seawater pumped from the Otago Harbour and maintained in the laboratory for at least one week prior to use in experiments. All experiments were carried out at 15 °C.

### *Distribution of chitons on the shore*

The number of chitons per square metre was measured using a quadrat 2 × 0.5 metres, placed at 1 metre intervals up to the shore at a site within the collecting area. All chitons within the quadrat were counted and the height of each sample noted. The results are expressed in the form of kite-diagrams (height up the shore from MWL vs. number of animals · m<sup>-2</sup>).

### *Calculation of dry weight of tissue*

Whole animals were dried for 24 hours at 60 °C and weighed (total dry weight), after which all tissue was removed by placing the animals in a concentrated solution of KOH. The remaining valves were then washed, dried, and reweighed.

Dry weight of tissue was calculated, plotted against total dry weight and the resultant regression lines (Table 1) were used for subsequent determination of tissue dry weights.

TABLE 1. Equations relating total dry weight to tissue dry weight for six species of chitons. Equations are for log-log plots of total dry weight (A; g) versus tissue dry weight (B; g).

Species	Equation	n	r
<i>Acanthochitona zelandicus</i>	$A = 0.565 B^{0.937}$	14	0.998
<i>Amaurochiton glaucus</i>	$A = 0.432 B^{0.960}$	10	0.991
<i>Cryptoconchus porosus</i>	$A = 0.678 B^{0.960}$	17	0.997
<i>Ischnochiton maorianus</i>	$A = 0.385 B^{1.190}$	11	0.994
<i>Onithochiton neglectus</i>	$A = 0.241 B^{0.908}$	9	0.985
<i>Sypharochiton pellerisepentis</i>	$A = 0.312 B^{0.860}$	13	0.980

#### *Aquatic respiration*

Aquatic oxygen consumption was measured using the method described by Taylor & Brand (1975 a, b) and Crisp *et al.* (1978). A Radiometer oxygen electrode was connected via a Radiometer pHm 71 Meter to a Smith's Servo-scribe chart recorder (adjusted to 100 mV). Animals in the size range 0.20-6.2 g total dry weight were used in experimental chambers ranging from 10-45 ml in volume with a single animal being used in each experiment. The animals were left in the chamber until they had attached to the resting platform prior to the start of experiments. Salinity was kept constant throughout the experiments. The results are expressed as ml O<sub>2</sub> consumed · h<sup>-1</sup> · animal<sup>-1</sup> (V<sub>O<sub>2</sub></sub>).

The effect of declining oxygen tension on the rate of oxygen consumption was determined by allowing the animals to deplete completely the oxygen supply within the chamber. Metabolites released from animals may interfere with the respiratory response using this method: however, Sassaman & Mangum (1972) concluded that the response of animals exposed to declining oxygen tension in sealed containers was due essentially to changes in oxygen tension. Oxygen consumption rates recorded in the bivalve *Arctica islandica*, also via the closed chamber method, were also found to be unaffected by metabolite build up (Taylor & Brand 1975). The weight specific oxygen consumption was calculated at 10% intervals of decreasing oxygen tension.

#### *Aerial respiration*

Oxygen consumption in air was measured using a Gilson differential respirometer. The animals were left in the experimental chambers until they had attached to the bottom of the vessel before beginning the experiments. The ani-

mals were then left for 1 hour after which oxygen consumed ( $\mu\text{l}$ ) was measured at 5 minute intervals for 45-60 minutes. Results are expressed as  $\text{ml O}_2 \text{ consumed} \cdot \text{h}^{-1} \cdot \text{animal}^{-1}$  ( $V_{\text{O}_2}$ ). Only the results from animals which remained inactive throughout the experiment were included in the final data, i.e. resting animals. All animals were observed to be respiring aerially with the mantle skirt lifted to expose the gills and in no case was there any water found in the mantle cavity.

## RESULTS

### *Distribution*

Fig. 1 shows the distribution of the six species of chitons with respect to vertical zonation. It can be seen that all species occur at the lowest tidal level and hence overlap in distribution; however, interspecific differences in the upper limits of distribution enables the six species to be placed in arbitrary tidal zones: low shore (*C. porosus* and *O. neglectus*), mid-shore (*A. zelandicus* and *I. maorianus*) and high shore (*A. glaucus* and *S. pelliserpentis*). It can also be seen from Figure 1 that, with the exception of *Ischnochiton*, those species occurring highest on the shore also appear in greater numbers than those species occurring lower on the shore.

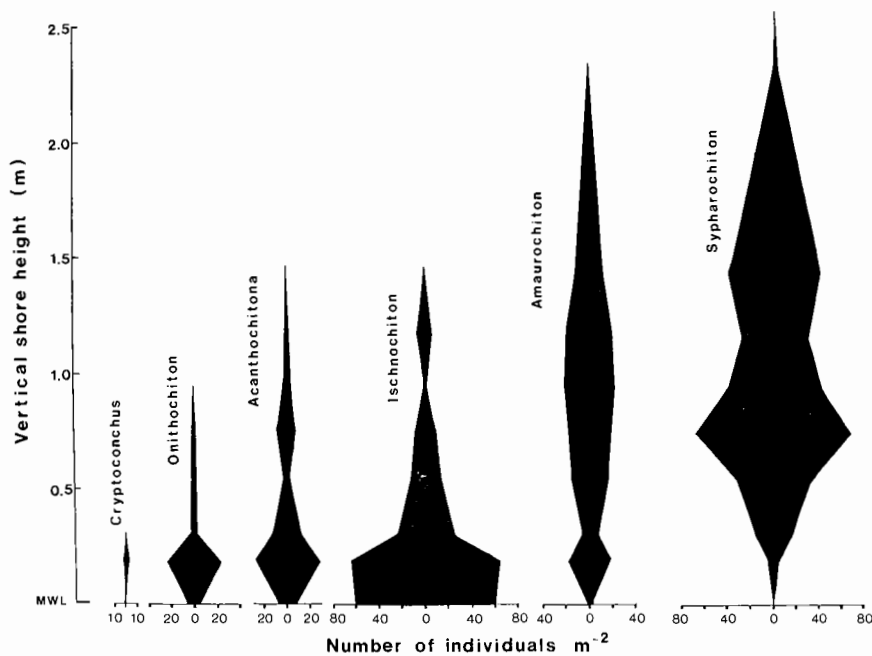


FIG. 1. Kite diagram showing intertidal distribution for the six chiton species.

The percentage time spent exposed to air for an average tidal cycle at the upper limit of distribution for each species is shown in Figure 2.




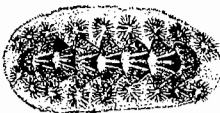
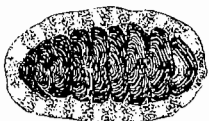

Species	% time exposed HWN - HWS	Aquatic equations	Aerial equations
 <i>S. pelliserpentis</i>	100 - 91.6	$Y = 0.063 X^{0.470}$ n = 19, r = 0.947	$Y = 0.117 X^{0.733}$ n = 23, r = 0.830
 <i>A. glaucus</i>	52.6 - 53.9	$Y = 0.091 X^{0.480}$ n = 19, r = 0.960	$Y = 0.124 X^{0.780}$ n = 26, r = 0.874
 <i>I. maorianus</i>	30.5 - 42.0	$Y = .111 X^{0.445}$ n = 13, r = 0.976	$Y = 0.120 X^{0.620}$ n = 21, r = 0.865
 <i>A. zelandicus</i>	30.5 - 42.0	$Y = 0.148 X^{0.448}$ n = 14, r = 0.989	$Y = 0.140 X^{0.820}$ n = 21, r = 0.815
 <i>O. neglectus</i>	0 - 2.6	$Y = 0.206 X^{0.399}$ n = 18, r = 0.921	$Y = 0.163 X^{0.738}$ n = 22, r = 0.747
 <i>C. porosus</i>	0 - 2.6	$Y = 0.253 X^{0.370}$ n = 17, r = 0.920	$Y = 0.127 X^{0.697}$ n = 21, r = 0.925

FIG. 2. Intertidal zonation, exposure times from extreme neap tides to extreme spring tides, and equations relating log dry weight to log  $V_{O_2}$  (aerial and aquatic) for the six species studied.

*Aquatic oxygen consumption*

Fig. 3 shows the relationship between oxygen consumption in air-saturated seawater and dry tissue weight for the six species of chitons studied. The data were fitted to the equation:

$$Y = aW^b \quad (1)$$

where  $Y$  is oxygen consumption ( $\text{ml} \cdot \text{h}^{-1}$ ),  $W$  is tissue dry weight (g),  $a$  is a proportionality factor and  $b$  is the weight exponent. The regression equation parameters are given in Fig. 2. Values for the weight exponent,  $b$ , ranged from 0.37-0.48.

Fig. 3 also shows that those species occurring highest on the shore (*S. pelliserpentis* and *A. glaucus*) have a lower rate of oxygen consumption in water than those species occurring lowest on the shore (*C. porosus* and *O. neglectus*), while the mid-shore species (*A. zelandicus* and *I. maorianus*) show rates intermediate between the high and low-shore species.

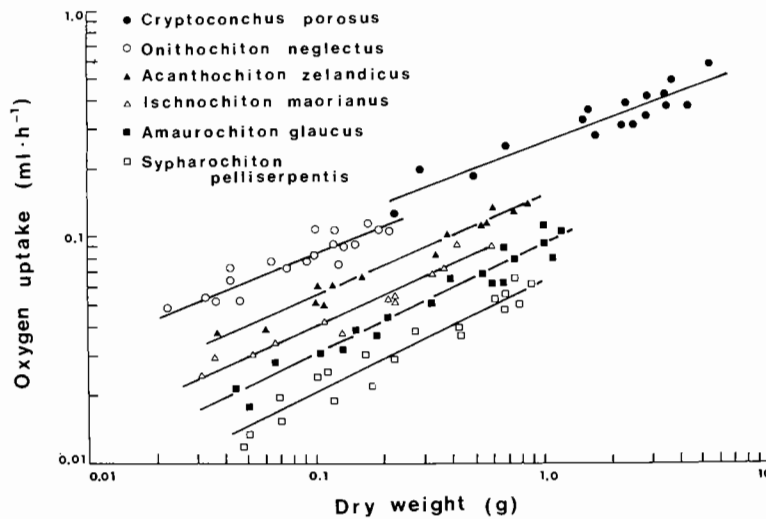


FIG. 3. Aquatic oxygen consumption by six species of chitons.

*Aerial oxygen consumption*

Oxygen consumption rates in air are plotted against dry tissue weight in Fig. 4. The data for each species were fitted to equation (1) as above and the regression equations are given in Fig. 2.

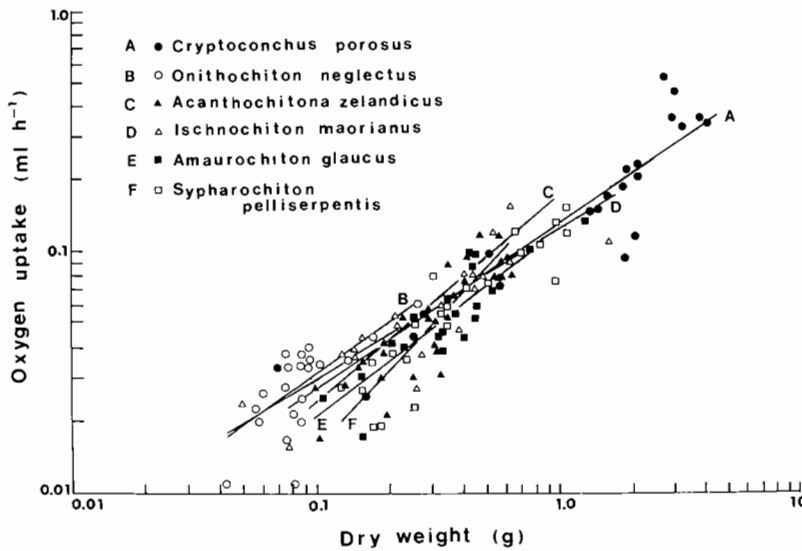


FIG. 4. Aerial oxygen consumption by six species of chitons.

Unlike the aquatic oxygen consumption rate, there appears to be no difference between high shore and low shore species in their oxygen consumption rates. In addition, the  $b$  value now ranges from 0.62-0.82.

#### *Aerial vs. aquatic oxygen consumption*

When aerial and aquatic regression equations are compared intraspecifically (Fig. 2), it appears that the high shore species (*A. glaucus* and *S. pelleriserpentis*) have higher oxygen uptake rates in air than in water, that the rates are approximately equal in the mid-shore species (*A. zelandicus* and *I. maorianus*) and that the low-shore species (*C. porosus* and *O. neglectus*) have higher rates in water than in air.

Oxygen consumption rates are, however, weight dependent. Solving the paired equations for aerial and aquatic  $O_2$  consumption for each species gives the weight at which the aerial and aquatic rates would be equal. Table 2 gives the weight for each species studied at which the rate of aerial oxygen consumption equals the aquatic rate. Thus, if an animal weighs more than the weight given in Table 2, the aerial oxygen consumption rate will be higher than the aquatic rate and conversely, if it weighs less than the weight given, the aquatic rate will be higher than the aerial rate.

It is also interesting to note that the weight at which aerial and aquatic rates are equal decreases from the low shore to the high shore species, i.e. only small individuals of the high shore species will have higher aquatic than aerial rates.

TABLE 2. Dry tissue weights for each species of chiton at which aerial oxygen uptake equals aquatic oxygen consumption.

Species	Weight (g)
<i>Sypharochiton pelliserpentis</i>	0.095
<i>Amaurochiton glaucus</i>	0.357
<i>Ischnochiton maorianus</i>	0.640
<i>Acanthochitona zelandicus</i>	1.162
<i>Onithochiton neglectus</i>	2.000
<i>Cryptoconchus porosus</i>	8.230

#### Statistical analyses

Differences in the intercepts ( $a$ ) and the slopes ( $b$ ) of the regression equations of oxygen consumption vs. tissue weight for both aerial and aquatic respiration were tested for significant differences (Wilson 1975) and the probabilities are shown in Tables 3a and b.

For aerial regression equations, *S. pelliserpentis* showed a significant difference in slope from *C. porosus* but there is no significant difference in slope between the other species combinations. *O. neglectus* shows a significant difference in intercept from *A. zelandicus*, *A. glaucus* and *S. pelliserpentis*. There is also a significant difference between the intercepts of *S. pelliserpentis* and *I. maorianus*, but there are no significant differences between the remaining species combinations.

For aquatic regression equations there was a significant difference in intercepts between all species combinations and the only significant difference in slopes was between *C. porosus* and *A. glaucus*. The probabilities for differences in intercepts ( $a$ ) and ( $b$ ) of the regression equations between aerial and aquatic respiration within species are given in Table 3. For *A. zelandicus*, *O. neglectus* and *C. porosus* there is a significant difference in intercepts and slopes. *S. pelliserpentis*, *A. glaucus* and *I. maorianus*, however, shows no significant differences in intercepts but significant differences in slopes, with the exception of *I. maorianus* which does not show a difference in slope. The species occurring higher on the shore (*S. pelliserpentis*, *A. glaucus* and *I. maorianus*) have respiration rates in air similar to those in water, whereas the lower shore species (*A. zelandicus*, *O. neglectus* and *C. porosus*) show significant differences in aerial and aquatic respiration rates.



TABLE 3a. Comparison of intercepts ( $a$ ) in six species of chitons. Probabilities for paired aquatic data are given above the diagonal line those for aerial values below the line.

	A	G	C	I	O	S	
A		0.000	0.000	0.000	0.000	0.000	
G	0.486		0.000	0.000	0.000	0.000	
C	0.760	0.389		0.000	0.013	0.000	aquatic
I	0.122	0.086	0.982		0.000	0.000	
O	0.003	0.016	0.350	0.628		0.000	
S	0.090	0.450	0.542	0.020	0.000		
							aerial

TABLE 3b. Comparison of slopes ( $b$ ) in six species of chitons. Probabilities for paired aquatic data are given above the diagonal line, those for aerial values below the line.

	A	G	C	I	O	S	
A		0.205	0.130	0.919	0.409	0.543	
G	0.629		0.017	0.316	0.053	0.633	
C	0.203	0.537		0.172	0.796	0.078	aquatic
I	0.070	0.242	0.479		0.264	0.647	
O	0.516	0.814	0.804	0.481		0.173	
S	0.377	0.205	0.021	0.007	0.201		
							aerial

A, *Acanthochiton zelandicus*    C, *Cryptoconchus porosus*    O, *Onithochiton neglectus*  
 G, *Amaurochiton glaucus*        I, *Ischnochiton maorianus*    S, *Sypharochiton pelliserpentis*

#### Oxygen consumption rates in declining oxygen tensions

Fig. 5 shows the results of five individual experiments for each species in which the relationships between the rate of oxygen consumption and the oxygen concentration of the external medium were studied.

The relationships between weight specific oxygen consumption and oxygen concentration for each species are shown in Fig. 6. Variations in the data due to weight differences were minimized by relating all  $V_{O_2}$  measurements to  $W^b$ , where  $W$  is the dry weight of tissue in grams and  $b$  is the value of the exponent relating  $V_{O_2}$  to body size, see Fig. 2 (Bayne & Livingstone 1977). By simple inspection, varying slopes for each species can be seen. The low shore species (especially *C. porosus*) show a slope approaching that of total oxygen dependence (oxygen conformer), as opposed to the high shore species' small slopes indicating oxygen independence.

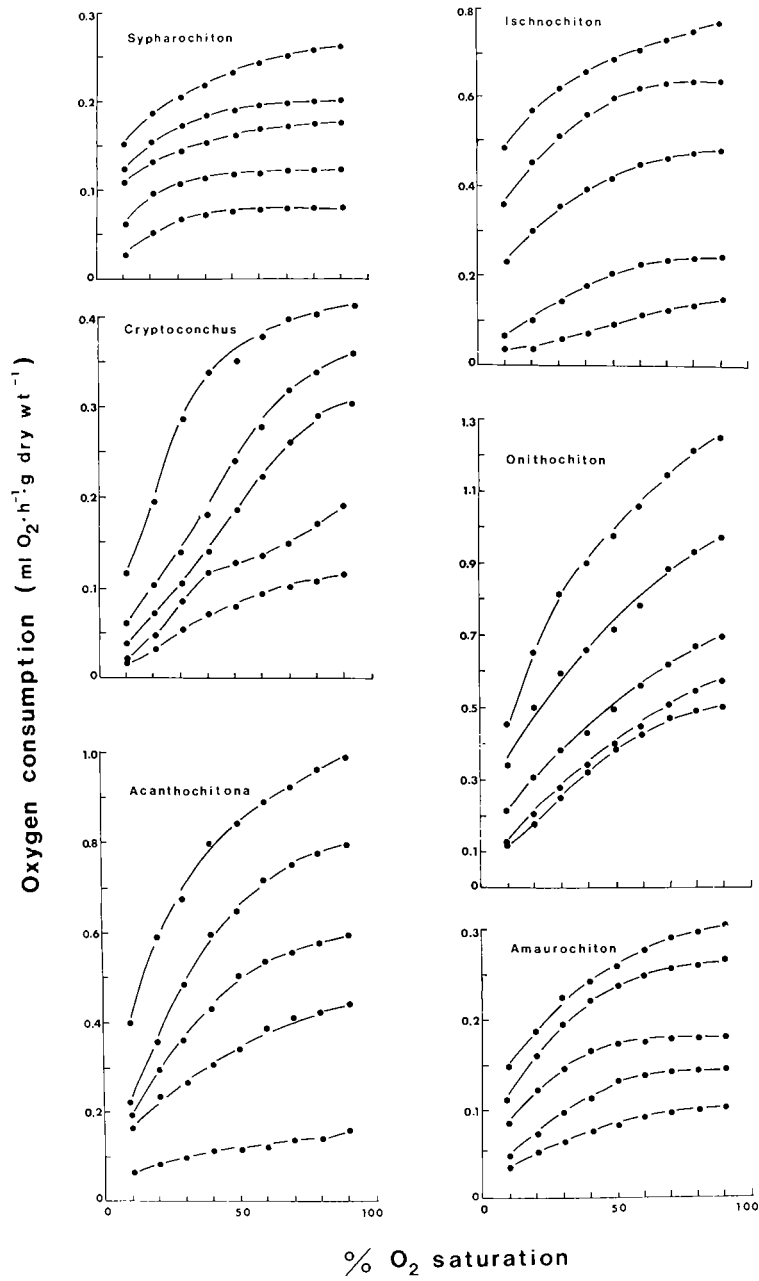


FIG. 5. The results of five individual experiments for each of the six species of chiton when exposed to declining oxygen tensions. Each family of lines represents a series of different weights.

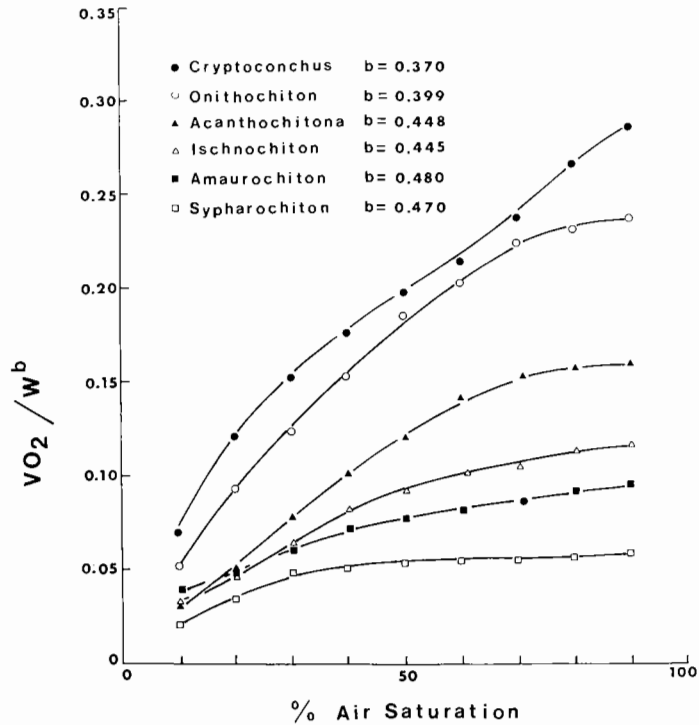


FIG. 6. The response of six species of chiton to declining oxygen tension.

It is difficult to determine the degree of respiratory dependence or independence on oxygen concentration, or any significant differences between species by simple inspection. However, a useful quantitative method for comparing the regulatory ability of marine invertebrates has been developed by Tang (1933) and Bayne (1973). Graphs relating the weight specific oxygen consumption ( $Q_{O_2}$ ) to oxygen concentration ( $P_{O_2}$ ) are expressed in linear form by plotting  $P_{O_2}/Q_{O_2}$  against  $P_{O_2}$ . This linear regression line has intercept  $K_1$  and a slope  $K_2$  which Bayne (1971) showed could be used to obtain an oxygen independence index  $K_1/K_2$ . The lower the value of this index, the greater the capacity to regulate oxygen consumption.

The ratio  $K_1/K_2$  is plotted against  $Q_{O_2}$  in Fig. 7 and the equations for the resultant regression lines are given in Table 4. This clearly shows that the six species may be divided into three groups with respect to their oxyregulatory capabilities and these three groups may be correlated with theoretical intertidal zones, i.e. high, mid and low shore zones. *C. porosus* and *O. neglectus* (low shore individuals) show little or no regulatory ability; *A. zelandicus* and *I.*

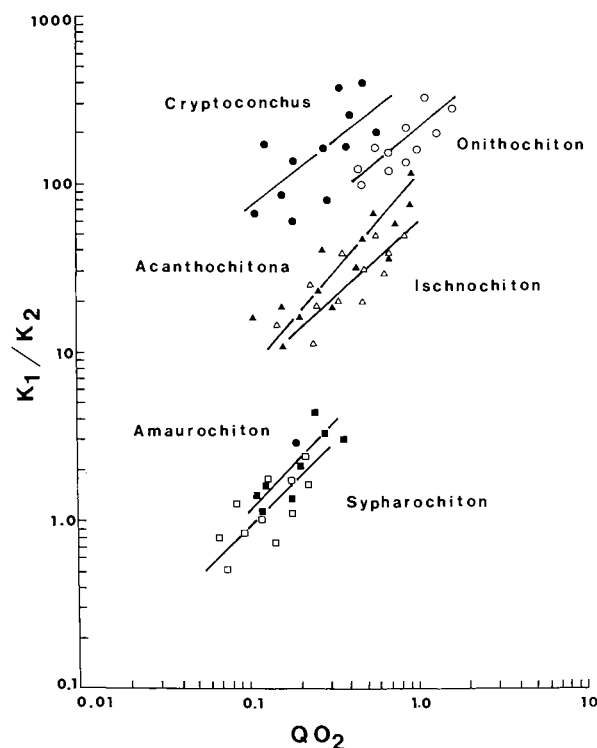


FIG. 7. The oxygen dependence index',  $K_1/K_2$ , plotted against the weight specific oxygen consumption.

*maorianus* (mid-shore) show a moderate degree of regulatory ability. The greatest degree of oxyregulation is shown by the two high shore species *S. pellerserpentis* and *A. glaucus*.

TABLE 4. Regression equations for  $K_1/K_2$ , the 'oxygen dependence index' against  $Q_{O_2}$ , the weight specific oxygen consumption.

Species	Regression equation	n	r
<i>Sypharochiton pellerserpentis</i>	$K_1/K_2 = 8.84 Q_{O_2}^{0.97}$	11	0.874
<i>Amaurochiton glaucus</i>	$K_1/K_2 = 11.90 Q_{O_2}^{1.04}$	9	0.890
<i>Ischnochiton maorianus</i>	$K_1/K_2 = 58.62 Q_{O_2}^{0.94}$	12	0.883
<i>Acanthochitona zelandicus</i>	$K_1/K_2 = 98.90 Q_{O_2}^{1.14}$	14	0.900
<i>Onithochiton neglectus</i>	$K_1/K_2 = 204.61 Q_{O_2}^{0.82}$	11	0.892
<i>Cryptoconchus porosus</i>	$K_1/K_2 = 397.67 Q_{O_2}^{0.766}$	12	0.656

## DISCUSSION

*Zonation*

Several authors have considered the effect of shore height on metabolic rate, although the functional significance of decreasing rate with increased shore height is not clear. Southward (1955) studied activity in several species of barnacles and maintains that the differences in activity from high and low tide levels may be as related to the difference in rate of growth, and possibly of general metabolism, as it is to temperature adaptations. Barnes & Barnes (1959) studied aquatic respiration in seven species of barnacles and found that the respiratory rates fell into a series in which the metabolic rate decreased from sublittoral to high intertidal species. They point out that stresses (e.g. temperature variations, desiccation and feeding opportunities) increase with increased shore height above low water level and suggest that these stresses are compensated for, at least in part, by a lower intrinsic metabolic rate as the species habitat moves from sublittoral to high intertidal. Sandison (1966) found that there was an apparent gradation in respiratory rate in which species inhabiting successively higher intertidal levels have higher rates of respiration in both air and water but dismissed the differences as a size effect. These readings were, however, based on averaged respiratory rates for what appears to be a size range of animals and dismissal of results on this basis appears unjustified. Shumway & Crisp (unpublished) have studied aquatic respiration in the same species of snails used by Sandison and found that there is indeed a gradation in respiratory rate with shore height, high shore species having a greater respiratory rate than low shore animals. Micallef & Bannister (1967) observed an inverse correlation between aquatic oxygen consumption and exposure in four species of British trochids and a direct correlation between aerial oxygen consumption and percentage exposure to air in their natural habitat. These correlations were attributed to adaptation of the respiratory mechanisms of the snails to benefit from the partial emancipation of the snails from seawater. Branch & Newell (1978) maintained that patterns of respiration in high and low shore limpets are related to food availability, as the problem of obtaining adequate food becomes severe for high intertidal animals and a low intrinsic metabolic rate for these species may act to conserve metabolic energy reserves.

Results from the present study indicate that aquatic respiration rates fall into a series in which consumption rate decreases from sublittoral species to high intertidal species (Figs 2 & 3), and that there are few interspecific differences in aerial respiration rates (Fig. 4, Table 4a). When aerial and aquatic respiration are compared intraspecifically, however, the results indicate that high shore species (*S. pelliserpentis*, *A. glaucus* and *I. maorianus*) have equal or higher respiration rates in air than in water, while low shore species (*A. zelandicus*, *O.*

*neglectus* and *C. porosus*) have higher aquatic rates than aerial rates. The low shore chiton *Cryptochiton stelleri* shows a higher aquatic respiratory rate than its aerial rate (Peterson & Johansen 1973), and Robbins (1975) has shown this also to be the case in *Nuttallina californica* and *Tonicella lineata*.

Table 3 shows that the comparison of aerial and aquatic oxygen consumption rates are weight dependent, i.e. large individuals of each species have higher aerial than aquatic rates of oxygen consumption. Hence for smaller individuals of each species, respiratory rate in water is going to be greater than in air. Size distribution data for all of the species studied here is unavailable; however, it is interesting to note that Boyle (1970) has shown that larger individuals of *S. pelliserpentis* occur higher on the shore than smaller individuals. The fact that small animals (occurring lower on the shore) respire faster in water, i.e. submerged longer, while large animals occurring high in the intertidal zone respire faster in air, has been shown in the limpet *Patella granatina* by Branch (1978). He attributes this to an exploitive strategy wherein the animals may maintain a consistently high level of respiration over their entire range.

The ability to respire in air involves a compromise between the access of air to the respiratory surface necessary for the maintenance of aerobic metabolism and evaporative water loss (which may result in desiccation) (Newell 1973). Boyle (1970) has shown that *S. pelliserpentis* can tolerate a substantial water loss under the effects of desiccation (a loss of 75% of the total body water could be tolerated before 50% mortality occurred). This was size dependent, smaller animals being affected by desiccation more so than large animals. As small individuals show a decreased aerial respiration rate and tolerance to desiccation, the two would appear to be correlated. Hence, the ability of an animal to respire in air will be dependent on its tolerance to desiccation and may, therefore, be a major factor in determining the vertical zonation of a species up the shore.

The present results are attributed to a combination of size distribution (migration up the shore with increasing size), food availability and temperature tolerance (desiccation), and more detailed studies of each of these aspects are needed before any generalization may be made.

#### *Effect of size on oxygen consumption*

In the equation oxygen consumption to body size,  $Y = aW^b$ , the weight exponent,  $b$ , varies considerably between species and experiments.

Very little information is available concerning oxygen consumption in chitons. Robbins (1975), and Peterson & Johansen (1973) studied aquatic and aerial oxygen consumption in chitons but Robbins does not show the relationship between body size and oxygen consumption and Peterson & Johansen do not report the aerial oxygen consumption-body weight relationship. For com-

parative purposes, extrapolation of the graph for aquatic oxygen uptake vs. body weight of the low shore chiton *Cryptochiton stelleri* from Peterson & Johansen (1973) gives an approximate  $b$  value of 0.64. Kincannon (1975) reported a  $b$  value of 0.73 for aquatic oxygen consumption in the low shore/-subtidal chiton *Tonicella lineata*. Recalculating the data of Nagabhushanam & Murti (1972) gives a  $b$  value of 0.43 ( $r = 0.97$ ) for the intertidal chiton *Chiton granoradiatus*.

The  $b$  values of aquatic oxygen consumption versus body weight of the six species studied here range from 0.37-0.48 (Fig. 2), while the aerial oxygen consumption rates versus body weight give  $b$  values of 0.62-0.82. The aquatic  $b$  values are lower than those found for *Tonicella* and *Cryptochiton*; however, in various invertebrates studied,  $b$  values may vary with temperature (e.g. *Littorina littorea*, Newell & Roy 1973), although Kincannon (1975) showed that in *Tonicella*  $b$  values did not vary significantly with temperature.

Toulmand (1967) has shown that in several species of *Littorina* the  $b$  values are much lower in water than in air. At 17.5 °C values ranged from 0.62-0.79 in air and from 0.34-0.55 in water. These are very similar to the results obtained here where  $b$  values in air range from 0.62-0.82 and from 0.37-0.48 in water.

The biological significance of  $b$  is still not clear, although it has been discussed by many authors (Zeuthen 1947, 1953, Hemmingsen 1950, 1960, von Bertalanffy 1957, Widdows 1978). Temperature, season and food level have all been shown to affect the value of  $b$  (Newell & Roy 1973, Bayne *et al.* 1973, Widdows 1978). In the case of the snails studied by Toulmond and the chitons in the present study, it would appear that the difference in 'aerial' and 'aquatic' represents a more fundamental factor at work and it is postulated that it is a difference in the surfaces available for respiratory gas exchange when these animals are exposed to water or air that may account for these differences.

#### *Effect of declining oxygen tension*

The degree of respiratory independence during periods of decreasing oxygen tension can be described by classifying animals as having an oxygen consumption independent or dependent on the ambient oxygen concentration. As pointed out by Mangum & van Winkle (1973) most species fall within the continuum between the two categories. Molluscs are known to range from dependence to independence (see Bayne 1967, 1971, Mangum & van Winkle 1973, Taylor & Brand 1975a, b). Although there are no known studies on the regulatory abilities of chitons, the six species studied here show varying degrees of respiratory independence. The  $K_1/K_2$  values (Table 4) indicate that the high shore species *S. pelliserpentis* and *A. glaucus* show the greatest respiratory independence; the mid-shore species *A. zelandicus* and *I. maorianus* show regulation to a lesser degree, while the low shore species *C. porosus* and *O. neglectus* show almost no

regulatory ability.

Various studies have shown that the ratio  $K_1/K_2$  decreases with decreasing  $Q_{O_2}$  (and therefore with increasing body size), i.e. the animals show an increasing respiratory independence with increasing size (Bayne 1971, Taylor & Brand 1975a, b, Shumway & Youngson 1979, Mackay & Shumway 1980). This was also found to be the case for the chitons studied here, each species showing increased oxyregulatory abilities with increasing size (see Table 4, Fig. 7).

As has also been shown for several species of bivalves (Bayne 1973, Taylor & Brand 1975), the six species studied here show a correlation between the possibility of experiencing hypoxia (e.g. possible stranding in anoxic water or mud at low tide) in the natural environment and their ability to regulate oxygen uptake. The low shore chitons have higher  $K_1/K_2$  values than the high shore species (see Table 4).

Taylor & Brand (1975b) pointed out that as respiratory independence increases with increasing body size, the above conclusions may be an oversimplification of the situation due to the fact that animals of varying size range (and therefore varying degrees of independence) occur together in the same habitat. However, as mentioned previously, Boyle (1970) found that for *S. pelliserpentis* there was a correlation between animal size and zonation height (i.e. larger animals were found further up the shore). This would appear to support further the conclusions of Bayne (1973), that intertidal animals develop a high degree of respiratory independence in response to the level of hypoxia experienced.

As with their aquatic and aerial respiratory rates, the respiratory response to declining oxygen tension appears to be related to the ability to regulate oxygen uptake increases with increasing height up the intertidal zone. This is perhaps what one might expect for a sheltered shore situation such as this, where those animals higher on the shore, stranded in small pools and in the sediment for longer periods at low tide are more likely to experience conditions of declining oxygen tension than those lower on the shore.

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