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Oxygen Consumption of the West African Blood Clam *Anadara senilis*

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Abstract

The West African blood clam *Anadara senilis* (L.) is one of a small number of bivalve species which have haemoglobin in their haemolymph. In the investigation reported here, in which the mussel *Mytilus edulis* (L.) was also studied for comparative purposes, it was shown that *A. senilis* was an oxygen regulator between oxygen tensions corresponding to 50 and 100% air saturation. Oxygen uptake increased by about 128% after 24 h at zero pO_2; although the haemoglobins of *A. senilis* were found to be responsible for about 34% of oxygen uptake at 25 °C (a proportion unaffected by pO_2), there was clearly insufficient haemoglobin present in the haemolymph to act as an effective oxygen store during prolonged exposure to anoxic conditions.

Introduction

The West African blood clam *Anadara senilis* occurs in many lagoons along the West African coast. Some of these lagoons are separated by sand banks from the sea for the greater part of the year. In the open lagoons, the clams are often emersed in near anoxic conditions in the mud at low tide, while they are bathed in fully oxygenated water at high tide. At low tide, they are also periodically (i.e., during the rainy season) covered by water of low salinity. Djangmah *et al.* (1979) showed that *A. senilis*, like many other bivalves, isolates its tissues from low salinities by closure of its shell valves. Bayne (1973) showed that, in full sea water (35‰ S), *A. granosa*, which also experiences hypoxic conditions, is able to regulate its oxygen consumption during hypoxia.

In the present study, we investigated (1) oxygen consumption of *Anadara senilis* in declining oxygen tension, (2) relationship between body size and oxygen consumption, and (3) effect on oxygen consumption of blocking the haemoglobins by carbon monoxide (see also Djangmah *et al.*, 1978). We also report on the size of the oxygen debt incurred by individual clams which had been without oxygen for various periods.

Materials and Methods

Collection and Maintenance of Clams and Mussels

Anadara senilis (L.) was collected from Elmina lagoon, near Cape Coast in Ghana and sent by air to the United Kingdom. In the laboratory, specimens were held in circulating seawater (33.5‰ S) at 25 °C, which is near to the native ambient temperature of 28 °C. Mortality was nil after the initial shock caused by transportation. For comparison purposes, specimens of *Mytilus edulis* (L.) were obtained from the shore of the Menai Strait, North Wales; they were held at 15 °C. Clams and mussels were fed daily on a mixed algal diet consisting of species of *Isochrysis*, *Tetraselmis* and *Skeletonema*, and were kept in the laboratory for several weeks before use in experiments.

Respirometry Measurements

Oxygen consumption in *Anadara senilis* and *Mytilus edulis* was estimated using a scaled-up version of the oxygen electrode technique described and evaluated by Davenport (1976). A Perspex vessel of 60 ml capacity was used. The radiometer oxygen electrode was connected via a radiometer PHM 71 Mk 2 pH meter to a Smiths Servoscribe chart recorder (adjusted to 100 mV) on which the oxygen tensions in the respirometer were displayed. To obtain oxygen consumption values for *A. senilis* and *M. edulis*, the following procedure was followed for each individual. The oxygen electrode, without its chamber, was suspended in temperature-controlled (25 °C for *A. senilis*, 15 °C for *M. edulis*), air-saturated, filtered seawater (33.5 ‰ S) and

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allowed to equilibrate for 10 min. The pH meter and chart recorder were then adjusted to give near full-scale chart deflection. The electrode was subsequently immersed in an oxygen-free solution of sodium dithionite in sea water; it was left to equilibrate for 10 min and the resultant chart trace was taken to represent 0% air saturation. The electrode was returned to air-saturated sea water and allowed to equilibrate once more. The chamber body was then filled with air-saturated sea water of appropriate temperature (25 ° or 15 °C), the clam or mussel was added, and the lid fitted (the seal between body and lid was made with a smear of silicon grease). The electrode was gently inserted into the tapered hole of the lid, and the assembly was placed in a temperature bath over an immersible magnetic stirrer. The respiration rate of the clam or mussel was expressed as a slope on the chart recorder trace, and the molluscs's oxygen consumption was calculated from this slope, the chart speed, the water volume of the chamber (allowing for the mollusc's own volume), and the known oxygen concentration corresponding to air-saturated sea water. Control experiments showed that the electrode's own oxygen consumption could be ignored. Total wet weights of clams and mussels were determined after respirometry. Soft tissues were freeze-dried and re-weighed.

Effect of Declining Oxygen Tension on Oxygen Uptake

The effect of oxygen tension (pO_2), expressed as per cent of air saturation, on respiration rate was determined as follows: 6 individuals between 0.401 and 0.567 g in weight of *Anadara senilis* were each placed, in turn, in the respirometer and allowed to respire until all oxygen had been removed (the respirometer was refilled with air-saturated sea water between each determination). From the chart paper traces, the respiration rates at 2, 5, 10, 20, 30, 40, 50, 60, 70, 80, 90 and 100% air saturation were calculated. Six more individuals, covering a much wider body size range were similarly treated to obtain data about the relationship between size and oxygen consumption in *A. senilis*.

Oxygen Debt

To establish whether *Anadara senilis* exhibited an enhanced oxygen uptake after a period of exposure to anaerobic conditions, the following experiment was made. Six clams (some of the 12 used in the declining oxygen tension experiment) were each left in the deoxygenated respirometer for 24 h. Each was then removed from the respirometer and placed in aerated sea water for 5 min before being returned to the respirometer, which had been refilled with air-saturated sea water. Trial experiments had shown that 5 min was sufficient time to allow for the expulsion of deoxygenated water from the mantle cavity. The respiration rate of the clams was again estimated.

Carbon Monoxide Experiment

The contribution of haemoglobin to oxygen uptake in *Anadara senilis* was assessed as follows. Five clams were placed in turn in the respirometer and, in turn, allowed to exhaust the available oxygen; their oxygen-consumption rates at 2 to 100% air saturation levels were established (the consumption rates at high oxygen tension were also used in the body size/oxygen consumption correlation). They were then held in filtered sea water for 15 min followed by 15 min in carbon monoxide-saturated sea water, before being returned to the respirometer which was filled with air-saturated sea water. Clams were allowed to gradually exhaust their oxygen supply, and their respiration rates were calculated at various oxygen tensions. After the experiment, samples of blood were checked spectrophotometrically for presence of absorbance bands typical of carbon monoxyhaemoglobin. All samples displayed such bands, which confirmed that the clams' haemoglobin had been blocked. Five specimens of *Mytilus edulis* whose oxygen consumption rates had already been estimated, were put in carbon monoxide-saturated sea water at 15 °C and the above procedure was repeated. Since *M. edulis* contains no haemoglobin, it was hoped that this experiment would allow an assessment of the general effects of carbon monoxide upon the tissues of bivalves.

Results

Effect of Declining Oxygen Tension on Oxygen Uptake

Fig. 1 shows how the oxygen uptake of *Anadara senilis* is affected by declining oxygen tension. The clam is able to regulate its oxygen uptake at maximal values when oxygen tension changes from full air saturation to 50% saturation. Between 50 and 10% saturation, oxygen uptake decreases linearly with oxygen tension; below 10% air saturation, there is a sharper decline in oxygen uptake; at 2% air saturation the clams are still able to take up oxygen at about 25% of the rate in 100% air-saturated sea water.

Effect of Body Size on Oxygen Uptake

Fig. 2 plots the logarithms of individual rates of oxygen uptake at air saturation for 17 clams against the logarithms of the dry soft-tissue weights. The regression of log oxygen consumption (V_{O_2} ml O_2 h^{-1}) on log body weight (W) produced the equation:

$$V_{O_2} = 0.583\ W^{1.02}.$$

The correlation coefficient r was 0.92 (significant at $P = 0.001$). The specific exponent of the weight, b, was 1.02 ± 0.109 (standard deviation) for 17 clams whose weights ranged from 0.126 to 0.567 g. Inspection of the

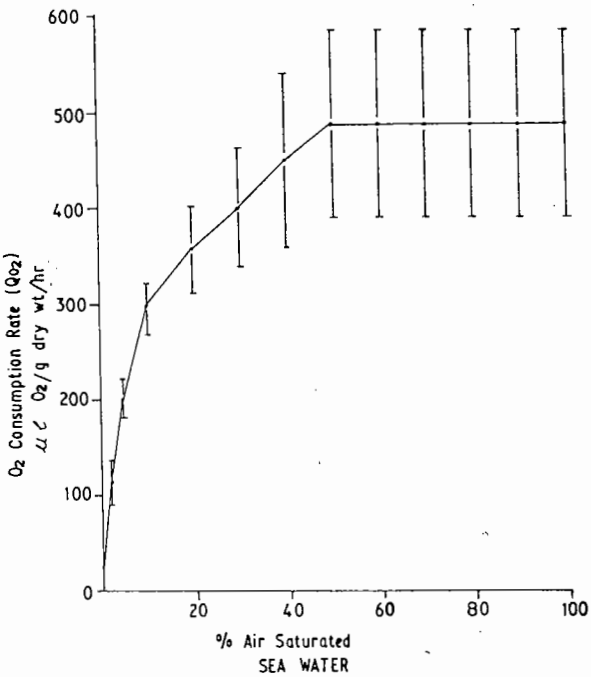

Fig. 1. *Anadara senilis.* O_2 consumption rate (Q_{O_2}) at 25 °C as a function of declining oxygen tension of sea water. Each point is mean of 6 clams ± 95% oxygen confidence limits. To obviate effect of body size, all individuals were within size range 0.401 to 0.567 g

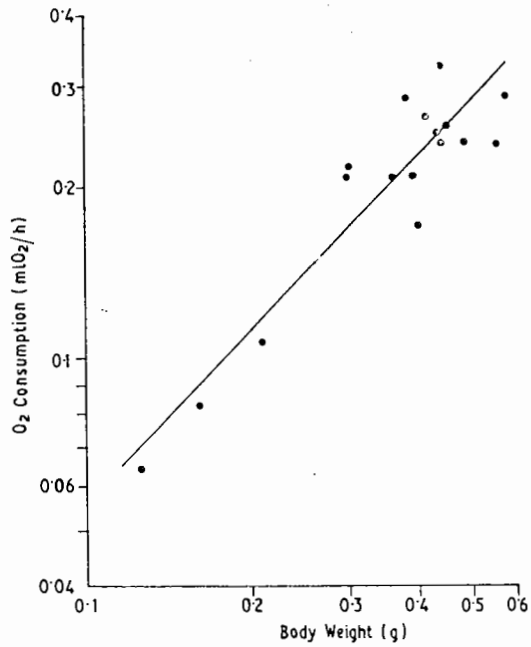

Fig. 2. *Anadara senilis.* Rate of O_2 consumption (V_{O_2}) of 17 individuals at 25 °C and 100% air saturation, plotted against dry tissue weight (g)

Table 1. *Anadara senilis.* Oxygen consumption rates (Q_{O_2}) before and after 24 h of anoxia: both sets of values were estimated at 100% air saturation. SE: standard error

Dry weight of clam (g)	Q_{O_2} (ml O_2 g^{-1} dry weight h^{-1})	
	before	after
0.4014	0.434	1.494
0.4371	0.330	0.716
0.5669	0.522	1.053
0.5450	0.434	0.918
0.2071	0.514	1.277
0.2980	0.696	1.223
Mean	0.488	1.114
± SE	± 0.123	± 0.277

equation above shows that the weight-specific oxygen consumption rate (Q_{O_2}) will not vary significantly with body weight. The mean Q_{O_2} calculated for the 17 clams was 0.579 ± 0.024 (standard error) ml O_2 g^{-1} dry weight h^{-1}.

Oxygen Debt

Table 1 summarizes the experiment on the degree of oxygen debt incurred by clams after 24 h at zero pO_2. The O_2 consumption (Q_{O_2}) of these 6 clams increased from a mean value of 0.488 to 1.114 ml O_2 g^{-1} dry weight h^{-1}, an increase of 128%.

Effects of Carbon Monoxide on Oxygen Consumption

Fig. 3 plots the O_2 consumption of *Anadara senilis* whose haemoglobin was blocked with carbon monoxide. Values are percentages of the mean O_2 consumption rate before treatment, at the given pO_2s. Oxygen uptake of individuals in fully saturated seawater were significantly reduced after haemoglobin blockage (Student's t = 9.79, $P < 0.001$). The percent reduction in O_2 uptake at known pO_2 values were compared by analysis of variance. The results of this analysis, summarised in Table 2, showed that the extent of the depression in O_2 uptake (mean 34% decrease) was not significantly dependent on pO_2.

The results obtained on exposure of *Mytilus edulis* to carbon monoxide were different (see Fig. 4). Above pO_2s of 30% air saturation, there was no significant difference in the O_2 uptake of mussels before and after carbon monoxide treatment. At lower oxygen tensions, O_2 uptake was significantly reduced after CO treatment. Q_{O_2} before and after CO treatment were compared by Student's t-test. The results are summarised in Table 3.

Discussion and Conclusions

This study has shown that *Anadara senilis* is similar to many other species of marine bivalves in its ability to regulate oxygen consumption in declining oxygen ten-

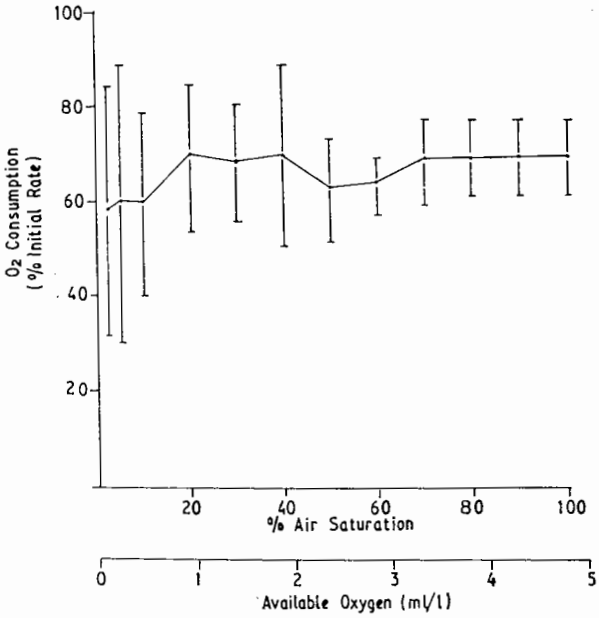

Fig. 3. *Anadara senilis.* O_2 consumption of CO-blocked clams at 25 °C as a function of declining pO_2: O_2 consumption, plotted as percent of mean initial O_2 consumption rate of unblocked specimens at the given pO_2s (lower abscissa). Each point is mean ± 95% confidence limits

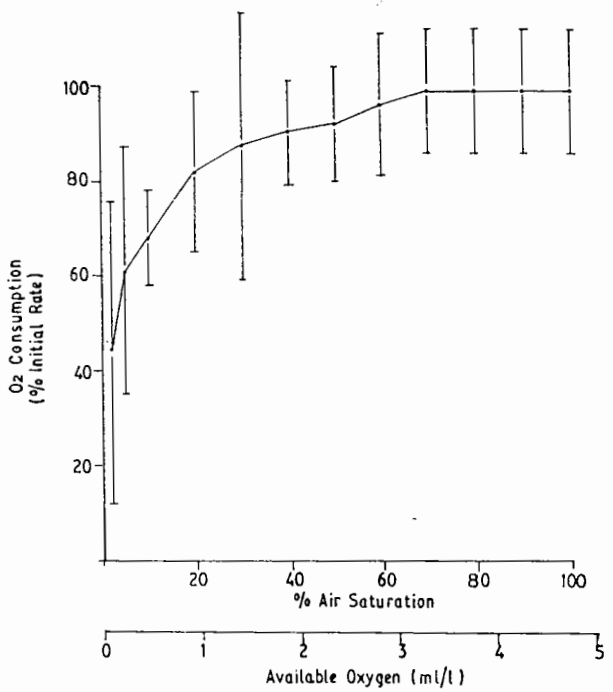

Fig. 4. *Mytilus edulis.* O_2 consumption at 15 °C after exposure to CO:O_2 consumption at each given pO_2, plotted as percent of rate before carbon monoxide treatment

Table 2. *Anadara senilis.* Analysis of variance of effect of carbon monoxide on O_2 uptake. For this analysis, percentages were converted into arcsine values. DF: degrees of freedom; SS: sum of squares; MS: mean square

Source of variation	DF	SS	MS
Between O_2 tensions	11	474	43.1*
Between individuals	4	1094	273.5**
Residual	44	2093	47.6
Total	59	3661	

*Not significant at P = 0.05
**Significant at P = 0.05

Table 3. *Mytilus edulis.* Comparison of Q_{O_2} before and after carbon monoxide treatment. For this analysis, Q_{O_2} values before and after CO treatment were paired

pO_2 (% air saturation)	Student's *t*	P
5	5.11	< 0.02
10	8.84	< 0.01
20	3.44	< 0.05
30	2.70	< 0.05
50	1.92	< 0.10
70	0.51	< 0.10

sions (Bayne, 1971, 1973). A related species, *A. granosa,* found in the mangrove swamps of Malaysia and Thailand regulates well at reduced oxygen tensions in water of full salinity (35‰) but markedly less so in dilute sea water. We have reported elsewhere (Djangmah *et al.*, 1979) that *A. senilis* closes its valves in reduced salinity.

The exact role of the haemoglobins in *Anadara senilis* is not clear (see also Djangmah *et al.*, 1978). When the haemoglobins are blocked, and therefore cannot combine readily with oxygen, oxygen consumption is maintained at about 70% of the rate before such treatment. The mean depression in rate of oxygen consumption caused by haemoglobin blockage does not vary significantly with ambient oxygen tension. The mean contribution of haemoglobin to oxygen consumption is about 34%. In the arcid clam *Noetia ponderosa* at 23 °C, the contribution of haemoglobin to oxygen consumption increases from about 20% at low pO_2 (10 to 20% air saturation) to 52% at full air saturation (Deaton and Mangum, 1976). At 10 °C, the haemoglobin of *N. ponderosa* was shown by the same authors to be responsible for half or more of the total oxygen uptake and this contribution changes little with pO_2. 10 °C is outside the physiological range of *A. senilis,* so no attempt was made to test clams at this temperature in the present study. In contrast to *A. senilis,* the effect of carbon monoxide on oxygen uptake in *Mytilus edulis* was not great, particularly above 40% air saturation. In the clam *Mercenaria mercenaria,* which has no haemoglobin, the oxygen consumption of intact individuals was not affected in the

presence of 4 ml CO l^{-1} (Deaton and Mangum, 1976). As shown in the present study, *A. senilis* survives a fairly long period of anoxia, and this adaptation may support this clam over a longer than usual period of exposure in the mud at low tide (e.g. during extreme spring tide). The total quantity of haemoglobin in the blood, estimated at slightly more than 1 g per 100 ml, cannot act as an oxygen store for long periods. The mean oxygen consumption (Q_{O_2}) of 17 clams measured at 25 °C was 579 μl g^{-1} dry weight h^{-1}. In the related haemoglobin-containing arcid clam *N. ponderosa* Deaton and Mangum (1976) reported a Q_{O_2} of 316 μl g^{-1} dry weight h^{-1} at 23 °C and 148 μl g^{-1} dry weight h^{-1} at 10 °C.

The weight exponent, b, in the regression of oxygen uptake (V_{O_2}) on dry weight, $V_{O_2} = aW^b$, was 1.02. This appears to be rather high, but bivalves are known to display much interspecific and intraspecific variation in the b exponent: values range from 0.16 to 1.02 (Bayne *et al.*, 1973; Widdows, 1978).

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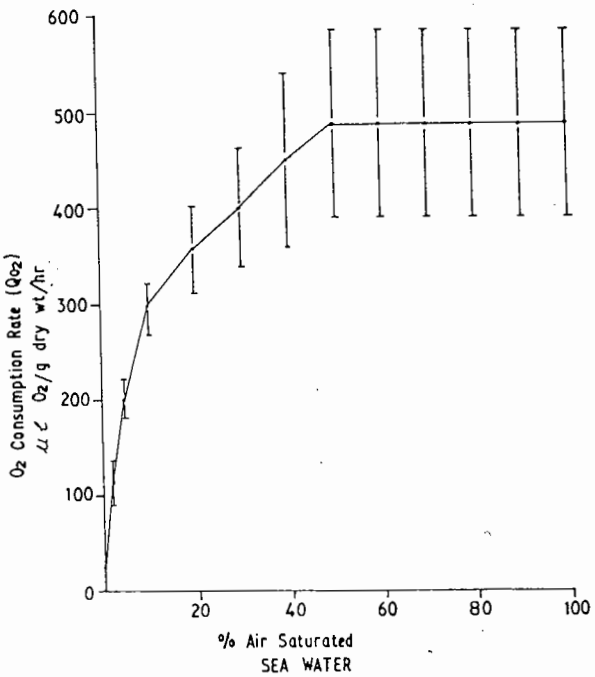

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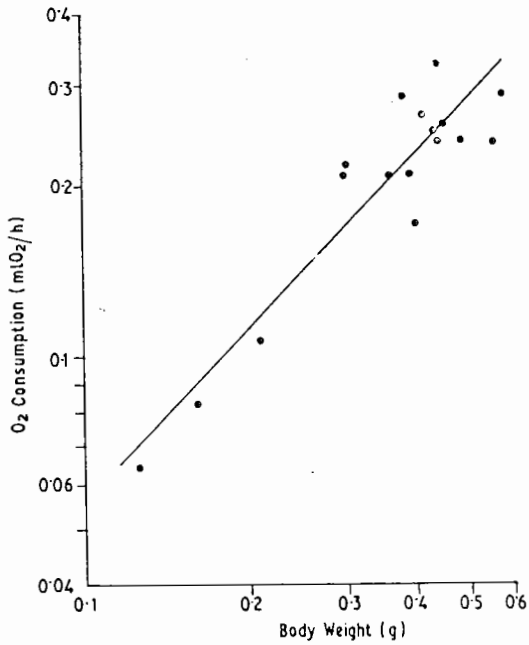

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Table 1 summarizes the experiment on the degree of oxygen debt incurred by clams after 24 h at zero pO_2. The O_2 consumption (Q_{O_2}) of these 6 clams increased from a mean value of 0.488 to 1.114 ml O_2 g^{-1} dry weight h^{-1}, an increase of 128%.

Effects of Carbon Monoxide on Oxygen Consumption

Fig. 3 plots the O_2 consumption of *Anadara senilis* whose haemoglobin was blocked with carbon monoxide. Values are percentages of the mean O_2 consumption rate before treatment, at the given pO_2s. Oxygen uptake of individuals in fully saturated seawater were significantly reduced after haemoglobin blockage (Student's t = 9.79, $P < 0.001$). The percent reduction in O_2 uptake at known pO_2 values were compared by analysis of variance. The results of this analysis, summarised in Table 2, showed that the extent of the depression in O_2 uptake (mean 34% decrease) was not significantly dependent on pO_2.

The results obtained on exposure of *Mytilus edulis* to carbon monoxide were different (see Fig. 4). Above pO_2s of 30% air saturation, there was no significant difference in the O_2 uptake of mussels before and after carbon monoxide treatment. At lower oxygen tensions, O_2 uptake was significantly reduced after CO treatment. Q_{O_2} before and after CO treatment were compared by Student's t-test. The results are summarised in Table 3.

Discussion and Conclusions

This study has shown that *Anadara senilis* is similar to many other species of marine bivalves in its ability to regulate oxygen consumption in declining oxygen ten-

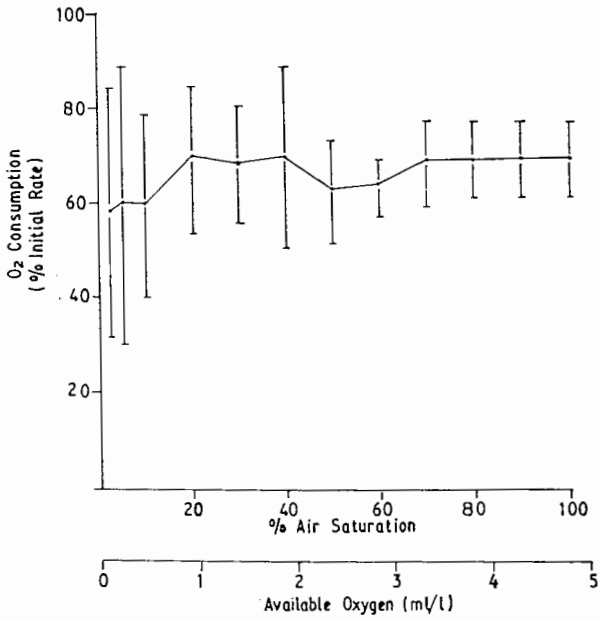

Fig. 3. *Anadara senilis.* O_2 consumption of CO-blocked clams at 25 °C as a function of declining pO_2: O_2 consumption, plotted as percent of mean initial O_2 consumption rate of unblocked specimens at the given pO_2s (lower abscissa). Each point is mean ± 95% confidence limits

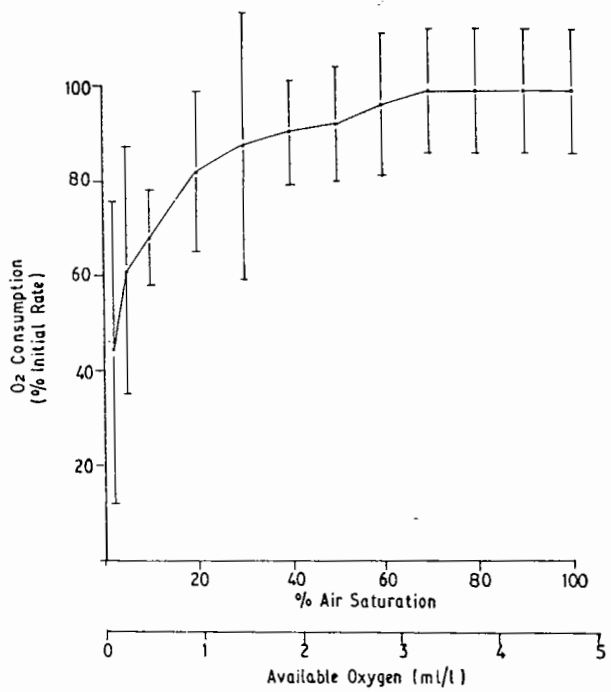

Fig. 4. *Mytilus edulis.* O_2 consumption at 15 °C after exposure to CO:O_2 consumption at each given pO_2, plotted as percent of rate before carbon monoxide treatment

Table 2. *Anadara senilis.* Analysis of variance of effect of carbon monoxide on O_2 uptake. For this analysis, percentages were converted into arcsine values. DF: degrees of freedom; SS: sum of squares; MS: mean square

Source of variation	DF	SS	MS
Between O_2 tensions	11	474	43.1*
Between individuals	4	1094	273.5**
Residual	44	2093	47.6
Total	59	3661	

*Not significant at P = 0.05
**Significant at P = 0.05

Table 3. *Mytilus edulis.* Comparison of Q_{O_2} before and after carbon monoxide treatment. For this analysis, Q_{O_2} values before and after CO treatment were paired

pO_2 (% air saturation)	Student's *t*	P
5	5.11	< 0.02
10	8.84	< 0.01
20	3.44	< 0.05
30	2.70	< 0.05
50	1.92	< 0.10
70	0.51	< 0.10

sions (Bayne, 1971, 1973). A related species, *A. granosa,* found in the mangrove swamps of Malaysia and Thailand regulates well at reduced oxygen tensions in water of full salinity (35‰) but markedly less so in dilute sea water. We have reported elsewhere (Djangmah *et al.*, 1979) that *A. senilis* closes its valves in reduced salinity.

The exact role of the haemoglobins in *Anadara senilis* is not clear (see also Djangmah *et al.*, 1978). When the haemoglobins are blocked, and therefore cannot combine readily with oxygen, oxygen consumption is maintained at about 70% of the rate before such treatment. The mean depression in rate of oxygen consumption caused by haemoglobin blockage does not vary significantly with ambient oxygen tension. The mean contribution of haemoglobin to oxygen consumption is about 34%. In the arcid clam *Noetia ponderosa* at 23 °C, the contribution of haemoglobin to oxygen consumption increases from about 20% at low pO_2 (10 to 20% air saturation) to 52% at full air saturation (Deaton and Mangum, 1976). At 10 °C, the haemoglobin of *N. ponderosa* was shown by the same authors to be responsible for half or more of the total oxygen uptake and this contribution changes little with pO_2. 10 °C is outside the physiological range of *A. senilis,* so no attempt was made to test clams at this temperature in the present study. In contrast to *A. senilis,* the effect of carbon monoxide on oxygen uptake in *Mytilus edulis* was not great, particularly above 40% air saturation. In the clam *Mercenaria mercenaria,* which has no haemoglobin, the oxygen consumption of intact individuals was not affected in the

presence of 4 ml CO l^{-1} (Deaton and Mangum, 1976). As shown in the present study, *A. senilis* survives a fairly long period of anoxia, and this adaptation may support this clam over a longer than usual period of exposure in the mud at low tide (e.g. during extreme spring tide). The total quantity of haemoglobin in the blood, estimated at slightly more than 1 g per 100 ml, cannot act as an oxygen store for long periods. The mean oxygen consumption (Q_{O_2}) of 17 clams measured at 25 °C was 579 μl g^{-1} dry weight h^{-1}. In the related haemoglobin-containing arcid clam *N. ponderosa* Deaton and Mangum (1976) reported a Q_{O_2} of 316 μl g^{-1} dry weight h^{-1} at 23 °C and 148 μl g^{-1} dry weight h^{-1} at 10 °C.

The weight exponent, b, in the regression of oxygen uptake (V_{O_2}) on dry weight, $V_{O_2} = aW^b$, was 1.02. This appears to be rather high, but bivalves are known to display much interspecific and intraspecific variation in the b exponent: values range from 0.16 to 1.02 (Bayne *et al.*, 1973; Widdows, 1978).

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