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THE EFFECTS OF OXYGEN CONCENTRATION AND ANOXIA ON RESPIRATION OF *ABARENICOLA PACIFICA* AND *LUMBRINERIS ZONATA* (POLYCHAETA)[1, 2]

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Animals respond in two general ways to a decrease in external oxygen concentration, *viz.*, they maintain the same respiratory rate independent of external oxygen concentrations down to a certain critical oxygen concentration (regulation) or their respiratory rate is directly dependent upon oxygen concentration (non-regulation) (Florey, 1966). Some examples of the effect of oxygen concentration on respiratory rate are reviewed by Beadle (1961).

When subjected to anoxic or nearly anoxic conditions, organisms will either undergo anaerobic metabolism, reduce their metabolic rate, or die. In the first case, partially oxidized end products can be accumulated in the organism, *i.e.*, the organism incurs an oxygen debt. Payment of the oxygen debt is indicated by an increased rate of oxygen uptake by the organism upon returning to aerobic conditions. Studies on the response of animals to anoxia have been reviewed by Brand (1944) and Beadle (1961).

The purpose of my studies was to measure oxygen concentrations in burrows of *Abarenicola pacifica* Healy and Wells at different stages of the tide; to investigate the effect of oxygen concentration on the respiratory rates of *A. pacifica* and *Lumbrineris zonata* (Johnson); and to determine if either species incurs an oxygen debt during anoxia. These worms live in large numbers at about +0.8 m above mean lower low water in muddy sand at False Bay, San Juan Island, Washington. Experiments were conducted during September 1968 to June 1969 at the Friday Harbor Laboratories, Friday Harbor, Washington.

The ecology of *A. pacifica* has been studied in False Bay by Hobson (1966, 1967). Lugworms irrigate their J-shaped burrows during high tide, drawing in overlying water, but not during low tide. Hobson (1966) demonstrated that *A. pacifica* performs aerial respiration, thus increasing its supply of oxygen at low tide. Wells (1945, 1949, 1953) has made extensive ecological observations on the related species, *Arenicola marina*. To my knowledge the only previous observations on *L. zonata* concern their geographic distribution (Hartman, 1944, 1948) and their rate of oxygen uptake in aerated water (Pamatmat, 1968; Banse,

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Nichols and May, 1971). Pamatmat (1968) has investigated physical and chemical parameters in False Bay and also the ecology and metabolism of the entire benthic community there.

Methods

Oxygen concentration in burrows

Laboratory studies were made in a tank of running sea water. Specimens of *A. pacifica* were allowed to establish burrows in sand from their habitat in the tank. The tank was drained for subaerial exposure of the burrows and was filled to simulate subaqueous conditions in the field.

The volume of water in a 10-cm deep burrow with a 2-gram worm was estimated to be 4 ml. Samples of water were obtained from burrows in both the field and the laboratory by inserting a 9-cm long, 15-gauge, hypodermic needle into a burrow and slowly drawing about 1 ml of sample into a 5-ml glass syringe. The tip of the needle was covered with 35-μ mesh nylon netting to preclude entry of sediment. Water from burrows was clear. If turbid water was withdrawn, indicating possible contamination by interstitial water, the sample was discarded. The dead space in the needle and syringe was filled with water from the same or an adjacent burrow. After removal of any bubbles of air from the sample, the syringe was immediately sealed with a toothpick and was placed in ice until the time of analysis (1 to 4 hr later). The samples were usually kept in the dark to prevent photosynthesis by microalgae included in the sample. Sediment temperature was measured by inserting a laboratory thermometer into the sand to a depth of 8 cm, the usual depth of sampling for water from burrows. Lugworms were usually below this depth.

In the laboratory the partial pressure of oxygen of the samples was measured with a Physiological Gas Analyzer, Model 160 (Beckman Instruments, Inc.) using a constant temperature bath, or with a Blood Micro System BM3 with Acid-Base Analyzer PHM71 (Radiometer A/S, Copenhagen, Denmark). Barometric pressure was measured with a Precision Microbarograph. The analyzers were calibrated with gas mixtures that had been analyzed with a 0.5-cc analyzer (Scholander, 1947) for the percentage of oxygen. To convert tensions to oxygen concentrations, it was assumed that the salinity of water in the field was 31‰, on the basis of the measurements of interstitial and overlying water in False Bay by Pamatmat (1968). Salinity in the sea water tanks was 30.5‰ in April and 30.0‰ in May. The oxygen concentration of sea water of known temperature and salinity in equilibrium with air was obtained from a nomogram based upon data from Green (1965).

Tests were run to determine whether the samples obtained from burrows were being contaminated with interstitial water. A solution of Evans blue dye was injected into the sand at several points 1 to 3 cm from a burrow in the tank, after which a sample was drawn from the burrow and its absorbance was measured at 602 mμ. At the same time a sample was taken from a burrow about 0.5 m away from the dye injection point as a control. These tests indicated that samples from lugworm burrows were not contaminated with interstital water.

Weights

Respiratory rates were calculated using wet weights. So that these data can be compared with data from other sources, the relationships between wet weight, dry weight, and ash-free dry weight were determined for *A. pacifica.* Prior to these determinations, worms were kept in sea water for at least 1 day to reduce the contents of their guts by defecation. Wet weights of *A. pacifica* were measured after blotting live specimens for a few seconds with absorbent tissue paper. Because of the small size of *L. zonata,* it was necessary to blot the live specimens for 5 minutes to obtain reproducible wet weights. Dry weights of *A. pacifica* were determined after drying at 80° C for 3 days, by which time the weight was constant. To determine ash content of lugworms, specimens were burned in a muffle furnace. The temperature of the furnace was increased gradually from 200° C to 500–550° C during an 8-hr period and left at 500–550° C for 8 hr more.

Respiratory rates

Specimens were all collected within a few meters of each other at about the 0.8-m tide level (100 m SW of Station 1 of Pamatmat, 1968) and in sediments that appeared similar in texture and color. For measurements of respiratory rates, worms were removed from sand in either the field or the laboratory and were placed in sea water for about 1 day in order to decrease the contents of their guts. Filtered sea water (Gelman glass fiber filter) was aerated and then siphoned into glass-stoppered (BOD), 300-ml bottles. Each test was made in the dark and consisted of at least one control bottle containing filtered water only and one experimental bottle with one or two *A. pacifica* or five to seven *L. zonata,* which were rinsed in filtered water before being put into the bottles. The tests lasted 0.9 to 3.5 hr for *A. pacifica* and 2.0 to 2.5 hr for *L. zonata.* The change in oxygen concentration during a test was not more than about 1.3 ml O_2/l for *A. pacifica* or not more than 0.6 ml O_2/l for *L. zonata.* At the end of the test, water was siphoned from the bottles and analyzed for oxygen concentration by the Winkler method. A 50-ml subsample was titrated with approximately 0.0085 N $Na_2S_2O_3$, standardized with 0.0100 N $KH(IO_3)_2$. Wet weights were measured at the end of an experiment (a series of tests on the same worms).

To study the effect of oxygen concentration on respiratory rate, rates of the same worms were measured repeatedly, using different initial oxygen concentrations. These were obtained by bubbling nitrogen gas through the water. In each experiment the order of the various oxygen concentrations was selected more or less randomly. Each experiment lasted from 1 to 4 days for *A. pacifica* or for 1 day for *L. zonata.*

The relationship between wet weight and respiratory rate of *A. pacifica* was determined by a total of 34 measurements of rate using 28 worms, collected and tested in February. In the aerated water used for all tests, oxygen concentrations ranged from 5.73 to 6.82 ml O_2/l, which is somewhat below the saturation values.

Oxygen debt

Experiments were run to determine whether the worms incurred an oxygen debt during anoxia and repaid this debt upon returning to aerated water. Their

respiratory rate was measured once or twice in aerated water to give initial rates; they were subjected to anoxia; then their respiratory rate was measured in aerated water immediately after they were removed from anoxia. Nitrogen gas was bubbled through sea water, resulting in an oxygen concentration of about 0.1 to 0.5 ml O_2/l. Worms were left in this water from 1 to 3 days. They can be assumed to have consumed the small amount of oxygen present within a short time after being placed in this low concentration and to have experienced anoxia for the remainder of the test. Consequently, the exact length of time in anoxia is not known. Measurements of oxygen concentration of the water in which the worms had been held resulted in values of 0.0 to 0.1 ml O_2/l. The Winkler method can be in error by 0.1 ml O_2/l at low-oxygen concentrations because of atmospheric contamination (Broenkow and Cline, 1969). In most cases a

TABLE I

Oxygen concentration in burrows of Abarenicola pacifica *in False Bay*

Date	Tide	N*	Oxygen concentration, ml O_2/l			Comments
			Mean	S.D.§	Range	
Apr 26	Low	6	0.76	0.20	0.66–1.16	On sand bar
Apr 26	Low	2	0.80		0.74–0.87	In tide pool
Apr 27	Low	5	0.79	0.35	0.49–1.35	One burrow only
Apr 27	Low	5	0.69	0.22	0.41–0.98	One burrow only
Apr 29	Low	5	1.17	0.45	0.60–1.79	On sand bar
Apr 29	Low	3	1.41	0.32	1.11–1.75	In tide pool
Apr 29	High	2	1.04		0.60–1.49	Early high tide
Apr 30	Low	4	0.90	0.39	0.46–1.35	On sand bar
Apr 30	High	2	1.88		1.25–2.50	Early high tide
Apr 30	High	4	2.49	1.10	1.39–3.93	Later high tide
May 1	High	8	2.08	1.02	1.50–4.35	Late high tide
May 21	High	7	2.93	1.28	1.28–5.31	Late high tide

* Number of burrows sampled (except where noted under Comments).
§ Standard deviation.

control set of worms in aerated water was run simultaneously with the experimental group to detect changes in respiratory rate due to causes other than oxygen deprivation, *e.g.*, starvation, absence of a burrow, or accumulation of metabolites in the enclosed water. The bottles of the control worms were kept unstoppered, and the water was aerated periodically by bubbling compressed air through the water.

RESULTS

Oxygen concentration in burrows

The results of measurements of oxygen concentration in burrows of *A. pacifica* in False Bay at low tide indicate that water in these burrows is never anoxic (Table I). The lowest value was 0.41 ml O_2/l. The mean value from Table I for low tide was 0.9 ml O_2/l. Twelve preliminary measurements in burrows in the field at low tide on September 20 gave a mean of 1.1 ml O_2/l. The mean

value from Table I for high tide was 2.3 ml O_2/l. The mean for early high tide was 1.5 ml O_2/l by comparison with a mean of 2.5 ml O_2/l for 19 measurements taken later in high tide. Because worms cannot irrigate their burrows until covered by water, they may not have completely flushed their burrows at the time the samples were taken during early high tide. The results of May 1 and May 21 suggests the highest values that might be expected, not only because the samples were taken near the end of high tide when the burrows probably were well irrigated, but also because the overlying water was observed to be supersaturated (6.53, 6.78 and 7.58 ml O_2/l or 132, 113 and 114 per cent saturation on May 21). Twelve measurements from three different burrows in the laboratory had a mean of 0.9 ml O_2/l for subaerial exposure, soon after the overlying water was drained off. Twelve similar measurements had a mean of 1.4 ml O_2/l for subaqueous conditions, which had been continuous for 1.5 days. The walls of the

TABLE II

Respiratory relationships of Abarenicola pacifica

Equation No.	Regression coefficients*				R^2	F	df
	a	b	c	d			
5	0.54	1.01			0.62	160.3	1,99
6	0.93	0.86	−0.51		0.70	28.4	2,98
7	−0.36	0.86	−0.38	1.33	0.74	14.0	3,97
8	1.49		−0.22		0.55	39.8	1,32

*See equation (4).

burrows in the field, though not always in the laboratory, are tan, indicating an oxidized lining in contrast with the dark gray reduced sediment beyond the burrows.

All of the 200 or more *L. zonata* excavated during low tide from the sand were found in the layer of gray reduced sand below the 2-cm-thick surface tan layer. The burrow walls of some worms were tan, although other walls were gray. I never observed any of their burrows to be continuous to the surface in the field. None of their burrows connected with the aerated burrows of *A. pacifica* or *Upogebia* sp. found in the same vicinity. Because some of the lumbrinerid burrows have tan walls, these worms must contact either the surface of the sand or at least the oxidized surface layer at some time. These worms in mud in the laboratory will readily burrow to the surface of the sediment; however, they rapidly retreat from the surface when they are disturbed.

Weights

Wet, dry, and ash-free dry weights were determined on 10 specimens of *A. pacifica* that had been kept in sea water for 1 day and on 12 specimens that had been kept in sea water for 5 days. The mean percentage dry weight of wet weight for the 22 measurements was 14.1 per cent with a standard deviation of 1.3 per cent, while the mean percentage ash-free dry weight of wet weight was 11.0 per cent with a standard deviation of 1.3 per cent. The percentage ash-free

dry weight of dry weight for the first set (75.6%) was significantly different from the value for the second set (79.5%) at the 1 per cent level ($t = 4.40 > t_{0.01} = 3.106$). On the basis of the percentages of ash-free dry weight of dry weight, it is probable that keeping the worms in sea water for longer than 1 day results in further defecation. The amount of additional defecation is so small, however, that it is almost inconsequential. Because many experiments lasted 3 or 4 days, a mean percentage for both sets of 77.7 per cent (standard deviation = 1.3%) ash-free dry weight of dry weight is probably most representative of the weight relationships of worms in these experiments.

Respiratory rate vs. oxygen concentration, weight, and temperature

Oxygen uptake rate can be expressed as a linear function of concentration for *A. pacifica.* Nineteen measurements of a representative 5.65-gram worm using a temperature range of 7.2 to 9.2° C and an oxygen concentration range of 0.43 to 6.45 ml O_2/l resulted in the following equation (Fig. 1):

$$R = 0.49 + (3.15)([O_2]) \tag{1}$$

where R is the oxygen uptake rate in microliters oxygen per gram wet weight per hour and $[O_2]$ is mean oxygen concentration for a test in milliliters oxygen per liter. The y-intercept is not significantly different from zero ($t = 0.155 < t_{0.50} = 0.689$) at the 50 per cent level. The correlation coefficient squared is 0.82, which shows that 82 per cent of the variability of respiration in this case could be explained by the variation of oxygen concentration. Another equation (Fig. 1)

$$R = 1.84 + (4.23)([O_2]) \tag{2}$$

resulted from 20 measurements on a 3.15-gram worm using a temperature range of 7.8 to 10.0° C and a range of oxygen concentration of 1.29 to 6.60 ml O_2/l. It is noteworthy that the slope is larger than in equation (1) because this worm was smaller. The correlation coefficient squared is 0.83. Both equations are significant at the 1 per cent level.

The relationship between respiratory rate and oxygen concentration, weight, and temperature is the following for *A. pacifica:*

$$R = 10^a[O_2]^bW^cT^d, \tag{3}$$

which also can be expressed in the following form:

$$\log R = a + b \log [O_2] + c \log W + d \log T. \tag{4}$$

On the basis of 101 measurements on *A. pacifica* from December 28 to March 23, a multiple regression of respiratory rate on oxygen concentration, weight, and temperature was computed. The regression has the form of equation (4) where W is wet weight in grams and T is temperature in degrees Celsius. Each step of the BIMED stepwise computation (Dixon, 1968) is shown in Table II as equations (5), (6) and (7), which are significant at the 1 per cent level. The ranges of the parameters are shown in Table III. Because the coefficient "b" in equation (5) is almost exactly one, oxygen consumption rate is in fact a linear function of oxygen concentration.

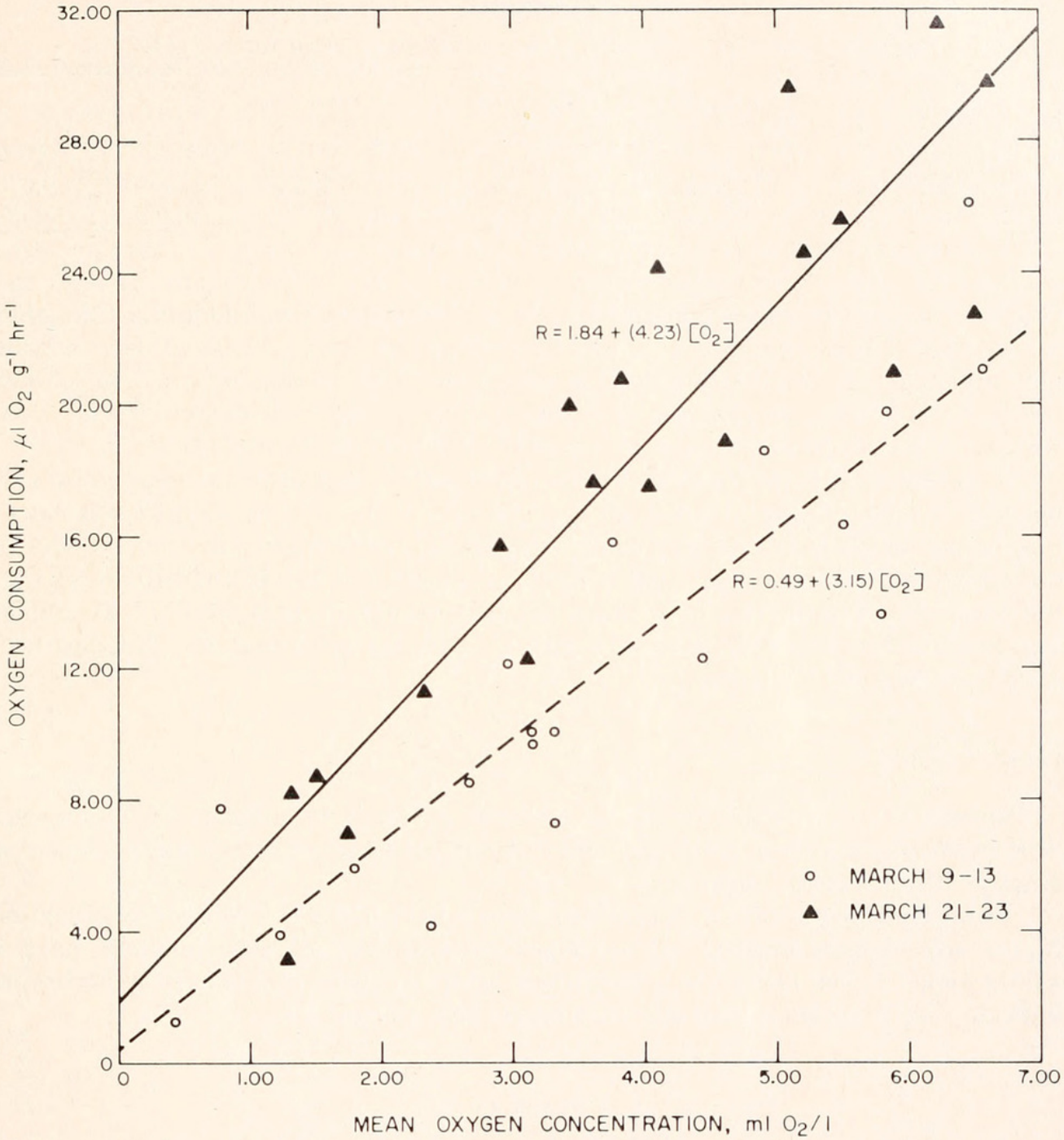

FIGURE 1. Oxygen consumption of *Abarenicola pacifica* as a function of oxygen concentration.

Equation (8) may also be expressed as

$$\log R' = 1.49 + 0.78 \log W \qquad (9)$$

where R′ is in microliters oxygen per worm per hr. The correlation coefficient squared for this equation is 0.94.

Using equation (7) a mean daily respiratory rate can be calculated for the period of late December through March 1969. Assuming a 2-gram worm, a temperature of 8° C, and an oxygen concentration of 2.3 ml O_2/l, the mean respiratory rate would be 21.6 μl O_2 $worm^{-1}hr^{-1}$ during high tide. For the same worm at low tide at 4° C and 0.9 ml O_2/l, the mean rate would be 3.9 μl O_2 $worm^{-1}hr^{-1}$.

TABLE III

Ranges of parameters and number of determinations for equations in Table II

Equation No.	$[O_2]$ range ml O_2/l	Weight range g	Temp. range C	N
5, 6, 7	0.43–6.71	1.18–7.52	6.1–10.0	101
8	5.73–6.82	0.20–6.33	7.1–8.4	34

Graphs of tidal height as a function of time were prepared from data in a tide table, assuming that tidal height is a sinusoidal function of time. These graphs indicate that organisms at the +0.8-m tidal level experienced an average of 6 hr of low tide and 18 hr of high tide per day during January through March 1969. Consequently, the mean respiratory rate would be 0.4 ml O_2 $worm^{-1}day^{-1}$.

In contrast with *A. pacifica*, *L. zonata* probably regulates its respiratory rate between 6 ml O_2/l and about 2 ml O_2/l, which is the critical oxygen concentration below which it is a nonregulator. Figure 2 shows the results for six sets of worms where the individuals had a range in mean wet weight of 0.16 to 0.21 g; the experiments were run in a range of temperature of 11.6 to 14.7° C and of oxygen concentration of 0.95 to 6.14 ml O_2/l. There were four to eight measurements on each set of worms.

Oxygen debt

Results of seven experiments to test the presence or absence of an oxygen debt in *A. pacifica* were equivocal and did not substantiate either the presence or absence of an oxygen debt.

Two experiments on *L. zonata* are shown in Table IV. With the exception of the second experimental in the second experiment, all experimentals have a substantially higher rate after anoxia than before. These preliminary experiments indicate that *L. zonata* contracts an oxygen debt during anoxia.

TABLE IV

Experiments on oxygen debt

Dates	Control or experimental	R, $\mu l\ O_2 g^{-1}hr^{-1}$			Duration of anoxia, hr
		Initial	Initial	Final	
Lumbrineris zonata					
Jun 5–7	Experimental	58.1	56.6	95.8	40
	Experimental	64.0	60.7	88.1	40
	Control	49.5	54.0	62.6	40
Jun 9–11	Experimental	48.2	55.4	82.5	50
	Experimental	68.3	74.5	78.7	50
	Experimental	53.1	60.5	96.9	50
	Control	57.6	59.0	57.6	50

Discussion

Comparison of measurements with the literature

Hobson (1967) determined the oxygen consumption rate as a function of weight for *A. pacifica* from False Bay. According to her results, a 2-gram worm in air-equilibrated water at 12° C would consume 66 μl O_2/hr. Using equation (7) above, the value would be 84 μl O_2/hr. The comparison of the latter value with Hobson's original data of oxygen uptake versus wet weight (Hobson, 1967, fig. 5) suggests that my rates are significantly higher than those of Hobson. Seasonal acclimation to temperature by *A. pacifica* might partially explain the dif-

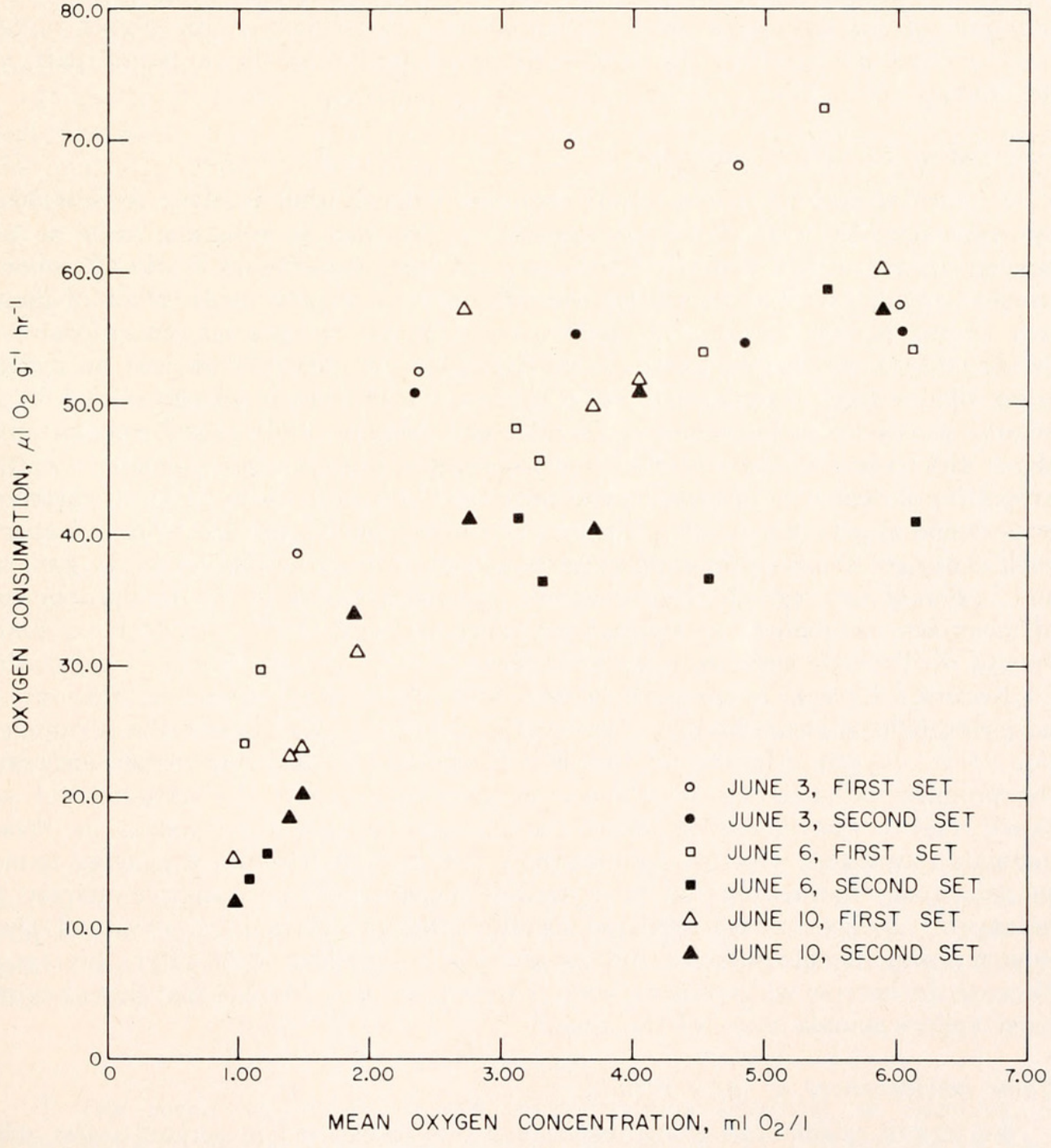

FIGURE 2. Oxygen consumption of *Lumbrineris zonata* as a function of oxygen concentration.

ference because her data were obtained in summer and fall, whereas my observations were made in late December to March.

Figure 2 shows that for *L. zonata* in the size range of 0.16 to 0.21 g, the average respiratory rate is about 50 μl $O_2 g^{-1} hr^{-1}$ or 9.5 μl O_2 $worm^{-1} hr^{-1}$ for a 0.19-gram worm above 2 ml O_2/l. Using a temperature of 13° C and Pamatmat's (1968) equation for respiratory rate of *L. zonata* from False Bay in well-aerated water ($\log R = -1.51428 + 0.73710 \log T + 0.64030 \log W$), the rate for a 0.19-gram worm would be 5.8 μl O_2 $worm^{-1} hr^{-1}$, which may be compared with 9.5 above. The data of Banse *et al.* (1971) are in agreement with Pamatmat's equation above. The comparison of my observations from Figure 2 with a graph of the original data by Pamatmat and by Banse *et al.* of oxygen uptake versus wet weight suggests that my rates are significantly higher than their rates. The durations of my tests were shorter than theirs. Consequently, the higher initial rates, caused by handling the specimens, were proportionally a larger part of the tests.

Adjustment to oxygen deprivation

A. pacifica and *L. zonata* adjust to oxygen deprivation in their environment by reducing their rate of oxygen uptake. *A. pacifica* is a nonregulator at all oxygen concentrations, whereas *L. zonata* is a nonregulator below 2 ml O_2/l, above which it regulates. The reason for the difference in respiratory behavior of these two worms is not obvious. It is possible that the oxygen concentrations experienced by *L. zonata* are lower, on the average, than those experienced by *A. pacifica*. The oxygen consumption rate of *L. zonata* may be constant above 2 ml O_2/l, because it may be unable to utilize the additional oxygen available at concentrations above this level. Measurement of internal oxygen concentrations in both species, properties of their blood pigments, and their total heat production by direct calorimetry should clarify the relationship between total metabolism (aerobic and anaerobic), oxygen consumption, and external oxygen concentration. Both *A. pacifica* and *L. zonata* may regulate their metabolic rate by increasing the relative proportion of anaerobic metabolism at low-oxygen concentrations (Dr. John Machin, University of Toronto, personal communication).

Because *A. pacifica* appeared healthy after three days in anoxia, they must have metabolized anaerobically. However, I could not demonstrate the accumulation of an oxygen debt during anoxia. It is possible that they either excreted the products of anaerobic metabolism or that they repaid the oxygen debt so slowly that I was unable to detect the increase in rate after anoxia by these methods (see Dales, 1958). Because the water in their burrows was never found to be anoxic, the reason for their well-developed ability to survive anoxia is unknown. *L. zonata* also appeared healthy after two days in anoxia, and preliminary experiments indicate the presence of an oxygen debt after this time. Because the burrow walls of many worms were gray, it is possible that these worms must endure anoxia some of the time.

Some consequences of these results

Results of calculations using respiratory rates measured in aerated water will be altered significantly by the data in this paper. Hobson (1967) calculated that

a 2-gram *A. pacifica* constantly in well-aerated water at 12° C would consume an average of 1.59 ml O_2/day. My calculated rate for a 2-gram worm is about 0.4 ml O_2/day. She measured the sediment turnover rate of *A. pacifica* (3.6 g sediment/day) and the average precentage of organic matter in sediment with dense populations (0.8%). Assuming a respiratory quotient of 0.8 and that one-half of the organic matter was organic carbon, she calculated the percentage removal of organic carbon from sediment (3.6%). Using a respiratory rate of 0.4 ml O_2/day, I obtain only 1.3 per cent. Both values of carbon utilization are minimum values since carbon may be used for growth, reproduction, and excretion as well as for respiration, which is a measure of maintenance only. In addition, the above calculation of carbon requirements is based only upon measurements of oxygen uptake and does not include carbon used in anaerobic metabolism, which may be important in this species. Nevertheless, the above values indicate that the food requirements of this species are low.

Banse *et al.* (1971) used data on respiratory rates of species of macrofauna and data on biomass at three stations in Puget Sound, Washington, to calculate the total respiration by macrofauna at these stations. They found that the total macrofauna at these stations only consumed between one-fifth and two-fifths of the oxygen consumed by the benthos in summer. They made all their measurements of respiration in water nearly saturated with oxygen. Because some of these species live in water low in oxygen, the actual rates of oxygen consumption are probably lower than the calculated rates. They calculated the total oxygen consumption for each species at each station. Having some knowledge of the microhabitat of each species, I could predict which species were likely to experience low oxygen levels. I then added all the oxygen consumption due to species ("major groups" only) in low-oxygen microhabitats and compared this figure to the "subtotal" in their paper, which represents all oxygen consumption by the "major groups" of macrofauna. Thus, I estimated that the minimum percentages of oxygen consumed at these stations by macrofauna likely to be living in low-oxygen microhabitats were as follows: Station 6, 40%; Station 7, 70%; and Station 11, 50%. Therefore, the relative proportion of oxygen consumed by macrofauna is probably less than that calculated in their paper.

In conclusion, I suggest that to obtain representative respiratory rates for energy flow studies involving organisms living in low oxygen, the effect of oxygen concentration on respiratory rate should be investigated.

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Summary

1. The mean values of oxygen concentrations observed in burrows of *Abarenicola pacifica* in False Bay were 0.9 ml O_2/l at low tide and 2.3 ml O_2/l at high tide.

2. Oxygen concentrations in burrows of *Lumbrineris zonata* were not measured, but burrow walls were often gray (reduced) although sometimes tan (oxidized).

3. For *A. pacifica* with nearly empty guts, dry weight is 14.1% of wet weight, ash-free dry weight is 11.0% of wet weight, and ash-free dry weight is 77.7% of dry weight.

4. The following respiratory relationships were found for *A. pacifica:* (a) Oxygen uptake rate can be expressed as a linear function of oxygen concentration at all oxygen concentrations up to 7.0 ml O_2/l. (b) The relationship between wet weight in grams after defecation and oxygen uptake in μl O_2 $worm^{-1}hr^{-1}$ is $\log R' = 1.49 + 0.78 \log W$. (c) The relationship between oxygen concentration in ml O_2/l, wet weight, and oxygen uptake in μl $O_2 g^{-1}hr^{-1}$ is $\log R = 0.93 + 0.86 \log [O_2] - 0.51 \log W$. (d) The regression of oxygen uptake on oxygen concentration, wet weight, and temperature in °C is $\log R = -0.36 + 0.86 \log [O_2] - 0.38 \log W + 1.33 \log T$.

5. During January through March, a 2-gram *A. pacifica* consumes 21.6 μl O_2/hr on the average during high tide and 3.9 μl O_2/hr during low tide or an average of 0.4 ml O_2/day.

6. *L. zonata* appears to regulate above about 2 ml O_2/l, below which it is a nonregulator.

7. *A. pacifica* is healthy after 3 days in anoxia; I was not able to determine if it incurred an oxygen debt during anoxia. *L. zonata* is healthy after 2 days in anoxia and probably incurs an oxygen debt, which it repays upon return to aerated water.

8. Calculations indicate that *A. pacifica* removes only 1.3% of the organic carbon from sediment it ingests.

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