The extraction of oxygen by estuarine invertebrates

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A few years ago we were attracted for several reasons to the
problem of measuring oxygen extraction rates, or the fractional
removal of oxygen from the incoming ventilatory stream. Generally,
the movement of water across sites of respiratory exchange with the
aquatic environment is caused by one of two kinds of mechanisms,
ciliary or muscular. One question that has been with us for a long
time concerns the adaptive determinants of flow rates in different
groups of animals. For example, ciliary flow is usually associated
with a straining device such as the lamellibranch gill which serves
a dual function, i.e., the water current brings the animal's food as
well as its oxygen. Indeed, most studies of ciliary flow have con-
cluded that the rate-determining factor, in the teleological sense,
is the animal's nutritional requirement rather than its respiratory
demand (Jørgensen, 1966).

Direct methods of estimating rates of oxygen extraction have
either involved some physical imposition on the animal's sensibili-
ties, such as catheterization of the siphon (a highly refined sense
organ) or else they have entailed discrete and therefore discontinu-
ous sampling of incurrent and excurrent fluid. In the first case,
the experience is clearly perceived by the animal and one must won-
der whether it results in any sort of feedback. In the second, the
oxygen regime at respiratory surfaces is portrayed acurately by a
feasible number of samples only if the flow rate does not change very
much in time. This lack of large-scale fluctuation on a short-term
basis is implicitly assumed to be true of ciliary flow, whose control

mechanism is unknown although evidence of central nervous input into the molluscan gill seems to be growing (Aiello, 1960). In contrast, if flow is intrinsically rhythmic in character, then oxygen extraction is almost certain to be poorly described by discontinuous samples unless an enormous number are subjected to time series analysis, a procedure that is not widely used by biologists. Spontaneously rhythmic currents are generated by muscular mechanisms in most lower metazoans, where the control center lies in endogenous pacemakers, and probably also in the holothurians (R. C. Newell, personal communication). As an alternative, oxygen extraction rates have been estimated less directly from separate measurements of ventilatory flow and oxygen uptake. This procedure is both tedious and complicated, due to rather arduous calibration and computation procedures (Dales, Mangum, and Tichy, 1970).

In the recent past, accurate measurement of the PO_2 of very small volumes of aqueous fluids has become routine. These measurements can be made by anaerobically procuring small samples, a necessarily discontinuous procedure, or they can be in situ, in which case they may be continuous. We initiated our studies on a group of marine invertebrates displaying different pumping mechanisms by making the measurements shown in Table 1, most of which derive from

TABLE 1
Oxygen extraction rates in marine and estuarine invertebrates exposed to well-oxygenated conditions

Species	Conditions	Incurrent PO_2 (mm Hg)	N	% Extraction (± S.E.)
Porifera				
Halichondria bowerbanki	20°C,running seawater	146	7	1.5 ± 1.0
Haliclona loosanoffi	22°C,running seawater	132	11	4.0 ± 1.0
Annelida				
Diopatra cuprea	22°C,natural tubes,still water	125	12	53.7 ± 6.0
	20°C,natural tubes,running seawater(Mangum, Santos,and Rhodes,1968)	140–145	78	39
Glycera dibranchiata	14°C,aerated aquarium	155–160	11	52.1 ± 7.3
	22°C,running seawater(Hoffmann and Mangum,1970)	140–145		58
Nereis virens	22°C,glass tubes, running seawater	146	15	22.0 ± 3.0

TABLE 1 (cont.)

Species	Conditions	Incurrent PO$_2$ (mm Hg)		% Extraction (± S.E.)
Pectinaria gouldi	22°C,natural tubes in sand, running seawater	146	14	9.0 ± 1.0
Mollusca				
Anadara ovalis	22°C,running seawater	157	16	5.0 ± 1.0
Busycon carica	18°C,aerated aquarium	159	7	31.5 ± 7.2
Dinocardium robustum	18°C,mixed aquarium	128	3	9.8 -12.8
Modiolus demissus	20°C,attached, running seawater	140	9	6.3 ± 0.4
Mytilus edulis	20°C,attached, running seawater	140	6	8.5 ± 1.0
Crustacea				
Upogebia affinis	22°C,burrowed in sand,running seawater	144	5	2.0 ± 1.0
Urochordata				
Ciona intestinalis	22°C,running seawater	153	14	4.0 ± 1.0

discontinuous samples injected into the PO$_2$ microelectrode chamber of our Radiometer blood gas machine (BMS1, equipped with Acid-Base Analyzer PHM71). The exceptions are in situ measurements from the mollusca *Busycon carica* and *Dinocardium robustum*, and the annelids *Diopatra cuprea* (Mangum, 1973) and *Glycera dibranchiata* (see below).

In general these estimates do not differ very much from those in the literature. If anything, those for animals with ciliary currents are lower than previous reports (Jørgensen, 1966). Among species with muscular ventilation, the only surprise is the very low figure for the ice cream cone worm, *Pectinaria gouldi*. To our knowledge, details of the function and pattern of the current in this species have not been reported; this worm may be an interesting exception to the annelid rule.

PASSIVE FLOW: ITS RESPIRATORY FUNCTION

We were particularly interested in the sponges and the annelids because of the intriguing suggestion by Vogel and Bretz (1972) that passive flow might aid ventilation of their respiratory surfaces. If fluid is moved along an unmoving surface bearing separate incurrent and excurrent openings to a tube below that surface, and if the

excurrent opening is elevated only slightly above the incurrent open-
ing, then fluid flow through the tube is caused by its boundary layer
properties. Previously it was pointed out (Hoffmann and Mangum, 1972)
that the model of passive flow is not applicable to annelids. The
tube or burrow is blocked by longitudinal muscle contractions that
maintain setal anchoring and cuticular contact at more or less regu-
lar intervals along the length of the body, known as the points
d'appui. Mechanistically, this occlusion is an inevitable consequence
of the mutually excitatory and inhibitory reflex pathways existing
between adjacent sets of body wall muscles. Teleologically, the worm
plugs its tube because it must work with the resistance of the bur-
row walls in order to maintain position at rest and to move substan-
tial volumes of fluid during a burst of pumping activity. Finally,
we pointed out that the importance of passive ventilation in sponges
needs quantitative evaluation, especially since current dogma holds
that actively generated currents in these animals are nutritive
rather than respiratory, a point with which Vogel and Bretz (1972)
agreed.

    With Dr. Vogel's help, we have attempted to make such a quanti-
tative evaluation. We set up several species in systems that meet
physical requirements for high velocity passive flow (Vogel, 1974),
and then made the measurements shown in Table 2, by anaerobically

TABLE 2
Oxygen extraction rates in marine and estuarine invertebrates under control
and passive flow conditions

Species	Conditions*	Incurrent PO_2 (mm Hg)	N	% Utilization (± S.E.)
Porifera				
Halichondria bowerbanki	Control	146	7	1.5 ± 1.0
	Passive flow	146	8	1.5 ± 1.0
Haliclona loosanoffi	Control	146	11	4.0 ± 1.0
	Passive flow	146	17	4.0 ± 1.0
Annelida				
Nereis virens	Control(bur-rowed in sand)	140	5	50.0 ± 2.0
	Passive flow	140	6	50.0 ± 2.0
Crustacea				
Upogebia affinis	Control(bur-rowed in sand)	144	5	3.0 ± 2.0
	Passive flow	144	6	1.0 ± 1.0

removing 200 µl samples from a site a few millimeters below the
excurrent aperture and comparing their PO_2 with that of samples taken
simultaneously from the incurrent stream.

    We could not detect a reduction in oxygen extraction rates under
conditions physically conducive to passive flow either in the sponges,

in which Vogel (1974) has shown that its magnitude is impressive, or in the polychaete *Nereis virens*, in which passive flow is blocked (Table 2). Had we continued sampling burrow fluid from the crustacean *Upogebia affinis*, we probably would have achieved the results of a significantly lower oxygen extraction rate under passive flow conditions when the number of observations (N) became sufficiently great to reduce the error. But in this species, oxygen extraction rates under both control and passive flow conditions are so low that the endeavor did not seem worthwhile.

We were prepared to concur that passive flow, whose velocity reaches very high values under the right conditions (Vogel, 1974), may be quite important for sponge nutrition but not for respiration. And then it occurred to us that we might have overlooked the most important condition of its importance: low oxygen, particularly in the estuary. Most estimates of oxygen extraction rates have been confined to animals exposed to air-saturated conditions, and the oversight is not entirely without reason. Flourishing populations of epifaunal ciliary pumpers are usually associated with well-oxygenated intertidal habitats like wharf pilings. But the distribution of estuarine species is somewhat distinctive. In the Chesapeake Bay system, for example, where the intertidal zone is small and hard substrata are scarce, these animals are most prolific at several meters depth below the halocline on oyster reefs and gorgonian skeletons. It is here, in a greatly attenuated two-layer transport system such as the estuary, that low oxygen conditions developing along with summer stratification (Carpenter and Cargo, 1957; Biggs, 1967) are very much a part of the normal living conditions of benthic species.

We chose several of these species and made in situ measurements of oxygen extraction with a PO_2 hypodermic microelectrode whose signal was amplified by a Beckman Model 160 Physiological Gas Analyzer. The microelectrode was gently positioned with a micromanipulator in the excurrent siphon while incurrent PO_2 was monitored simultaneously with a macroelectrode (Yellow Springs Instrument Co. Model 5420). PO_2 was altered by bubbling nitrogen gas (Matheson Gas Products) or air through the water in a closed aquarium, and mixing it with submersible magnetic stirrers.

We quickly learned that the notion of continuous rates is quite inapplicable to most species, even when both incurrent and excurrent channels appear to be fully open (Fig. 1). Consequently, our data are computed where possible from the integral or estimate of the area under a continuous trace of PO_2 as a function of time (Yellow Springs Instrument Co. Models 80 and 81 recorders). We found, however, that the excurrent stream of many lamellibranch molluscs changes direction with such frequency that continuous traces spanning more than a few minutes are not reliable. Even though measurement was continuous, these data are given as discrete points which were noted simultaneously with visual confirmation that the microelectrode was in the appropriate position a few millimeters within the siphon and not touching its inner walls. Oxygen extraction rates in the soft-shelled clam *Mya arenaria* increase exponentially as the animal

encounters low oxygen levels, but they never reach very impressive proportions before the clam ceases pumping (Fig. 2A). At least one

Fig. 1. Record of PO_2 in excurrent channels of A) *Dinocardium robustum* (incurrent PO_2=160 mm Hg), B) *molgula manhattensis* (incurrent PO_2=160 mm Hg), and C) *Adocia tubifera* incurrent PO_2=45 mm Hg) in mixed aquaria at 19°C.

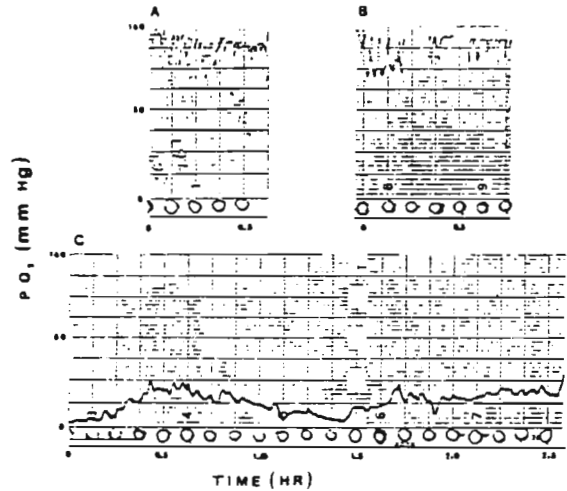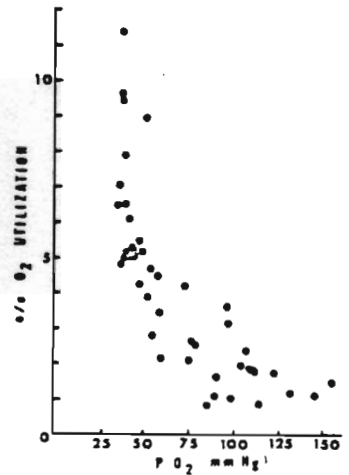Fig. 2A The fractional extraction or utilization by *Mya arenaria* of oxygen available in the incurrent ventilatory stream at 16°C and 20 o/oo.

very common natural event elevates those rates, however, The clam is exquisitely sensitive to vibration and other forms of mechanical stimuli, to which it responds by briefly withdrawing its siphons, thereby shutting off flow across its gills. After a period of siphon retraction lasting only a few seconds, oxygen extraction is enhanced to the point that respiratory function of the current is clear. The data in Figure 2B were obtained after inducing siphon retraction by gently tapping the side of the aquarium, a mode of stimulation that must occur frequently in the natural habitat.

Possibly the most interesting lamellibranch in the present context is the oligohaline clam *Rangia cuneata*. Its anaerobic metabolism, which has been studied in detail by Awapara and co-workers, differs in important respects from classical vertebrate glycolysis.

Fig. 2B. The fractional extraction or utilization of oxygen by *M. arenaria* after brief periods of siphon retraction. Incurrent $PO_2 =$ 86 mm Hg.
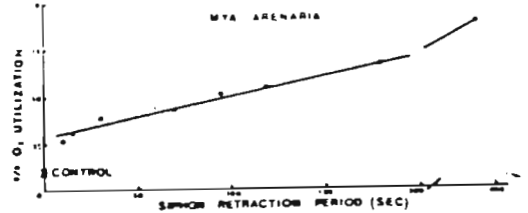
Perhaps its most bizarre feature is that anaerobic pathways continue to operate under well-oxygenated conditions (Chen and Awapara, 1969). Yet its rate of aerobic metabolism is quite typical for a lamellibranch mollusc of its body size. Figure 3A shows the effect of declining oxygen levels on aerobic metabolism before and after a 6-hr period of anoxic exposure. The aerobic metabolism before the anoxic exposure resembles that of *Mya arenaria* (Fig. 2C).

Fig. 2C. Oxygen uptake by *M. arenaria* under declining oxygen conditions.
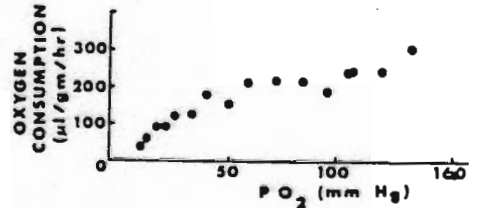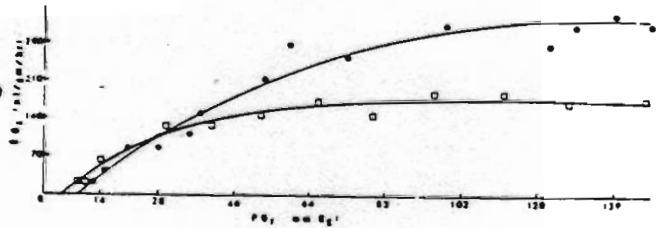

Fig. 3A. Oxygen consumption as a function of PO_2 in *Rangia cuneata* at 2 o/oo and 22°C before (o) and after (□) a 6-hr period of anoxia.


The data were calculated from the slope of the line describing oxygen depletion in a closed container (Yellow Springs Instrument Co. Model 5420 Polarographic Electrode). Since the exterior of the shell had been coated a week previously with paraffin wax (Kushins and Mangum, 1971), oxygen uptake cannot be attributed to microorganisms inhabiting the hard parts. In this particular example, the rate of aerobic metabolism was decreased by the anoxic experience, but that result is not consistent. When we analyzed paired observations on nine animals, we found no significant overall change (Mangum and Van Winkle, 1973). More important, the oxygen extraction rate is typically lamellibranch and minuscule (Fig. 3B). Unlike the results for the more polyhaline *M. arenaria*, the values for *R. cuneata* begin to reach respectably respiratory levels at low PO_2 values known to occur in the habitat for several months of the year (Carpenter and Cargo, 1957; Biggs, 1967).

We are left with the paradox of an animal that removes only a tiny fraction of the oxygen molecules available at its gill, although it burns quite a lot, and at the same time it is believed to operate anaerobic pathways at a high level (Chen and Awapara, 1969). While the relative magnitudes of contributions from aerobic and anaerobic

pathways to the overall energy budget cannot at present be gauged, we are unable to reconcile these rates with the concept of an essentially anaerobic organism. Instead, we should at least consider the possibility that the key to understanding the anomaly lies in the oligohaline habitat. In the Chesapeake Bay system, *R. cuneata* is

Fig. 3B. The fractional extraction or utilization by *R. cuneata* of oxygen available in the incurrent ventilatory stream and at 2 o/oo and 14°C under declining (o) and rising (Δ) oxygen conditions.
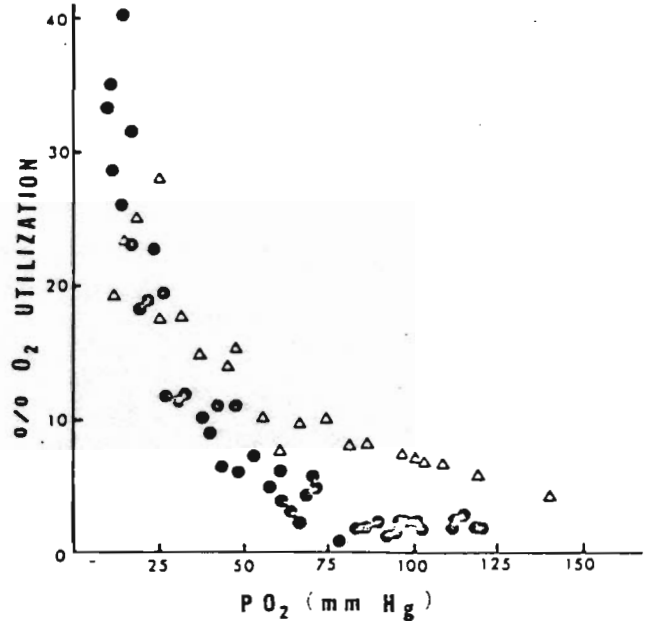
restricted to salinities below about 12 o/oo, and it becomes most abundant below 5 o/oo. One of its chief anaerobic pathways involves the conversion of pyruvate to alanine (Stokes and Awapara, 1968); regulation of free amino acid content is, of course, the major means of osmotic adjustment in molluscan tissue. Moreover, Anderson (1974) has shown that the clam is hyperosmotic to its dilute environment. This reaction may very well be more crucial in opposing diminution of the free amino acid pool in this very rigorous habitat than in the energy budget.

The hard-shell clam *Mercenaria mercenaria* yields a somewhat different result. In this case we were able to record excurrent PO_2 continuously, so the data in Figure 4A were computed from integrals.
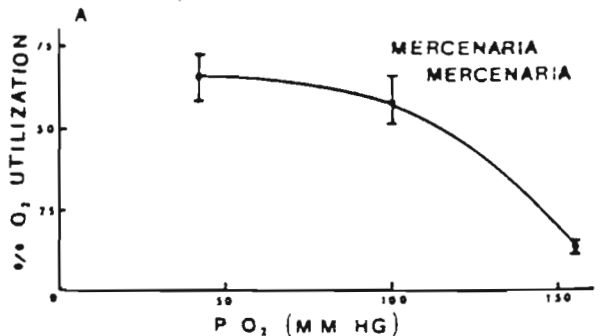

Fig. 4A. Oxygen extraction rates at 19°C in *Mercenaria mercenaria*.

Oxygen extraction reaches high values at intermediate PO2 values and
essentially ceases at low ones. Since we found that siphon retrac-
tion elevates these rates in *M. arenaria*, high values may be related
to the lower frequency of pumping periods than in the other clams.
Diving observations lead to the belief that pumping is more nearly
continuous in nature than in the laboratory, but we have observed
animals in nature only under well-oxygenated conditions.

The estuarine sponge *Adocia tubifera* (Fig. 4B) has much higher
oxygen extraction rates than its close relative *Haliclona loosanoffi*

Fig. 4B. Oxygen extraction
rates at 19°C in *Adocia
tubifera*.
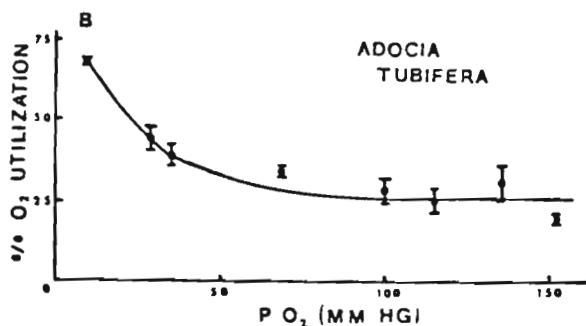
(Table 1). The rates do not change markedly until the animal
encounters low PO2, when they ascend to values more commonly associ-
ated with muscular mechanisms of ventilation. The same picture emer-
ges for the mesohaline tunicate *Molgula manhattensis* (Fig. 4C), in

Fig. 4C. Oxygen extraction
rates at 19°C in *Molgula
manhattensis* and *Styela
plicata*.
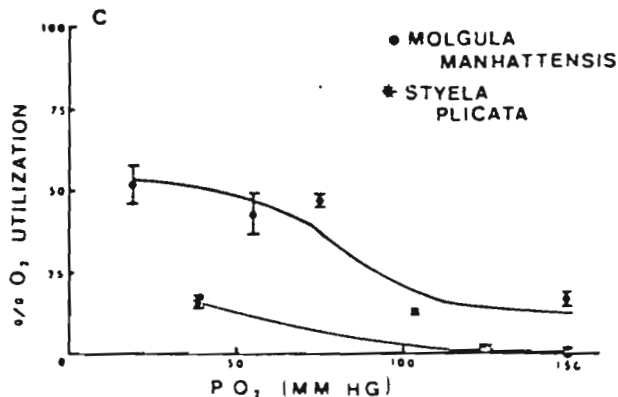
which the data suggest a rather abrupt change at intermediate PO2
from lower to higher rates. At this point, we wondered whether
higher values might not be an inevitable outcome of the computation
procedure rather than a distinctive feature of estuarine animals. So
we made another set of measurements on a more euhaline tunicate,
Styela plicata (Fig. 4C), and reassured ourselves that the low rates
obtained previously (Table 1) do in fact exist.

To summarize, under well-oxygenated conditions animals with ciliary mechanisms of generating water currents extract a fraction of oxygen from incurrents that is too small to reconcile with the concept of flow rate determination in response to respiratory demands. Consequently, adaptation of habit or body architecture to meet physical conditions requisite for high velocity passive flow cannot be understood in respiratory terms. However, in species characteristically reaching maximum abundance on the bottom of meso- and oligohaline regions of estuaries, where summer stratification produces very low oxygen environments, the oxygen extraction rate is appreciably elevated at lower PO_2's. While the generalization is severely limited by the number of species studied, this adaptation of at least several conspicuously dominant estuarine species enables them to cope with a special feature of their habitat other than its more obvious and better known osmotic properties. And in those estuarine species whose design meets physical requirements, passive as well as actively generated flow may make important contributions to respiration.

THE COST OF MUSCULAR VENTILATION

In a group of animals with muscular mechanisms of generating ventilatory flow, we took advantage of the very convenient rhythmicity of annelid ventilation to estimate its cost to the animal. When the microelectrode is inserted into the tube or burrow of an infaunal annelid, the rhythmic change in PO_2 reflects the alternating bursts of pumping activity and rest. The chronology of the rhythm and, therefore, changes in oxygen content at the site of gas exchange vary in different species. Our particular example is from the bloodworm, *Glycera dibranchiata* (Fig. 5); the pattern in the onuphid polychaete *Diopatra cuprea* is quite different (Mangum, 1973).
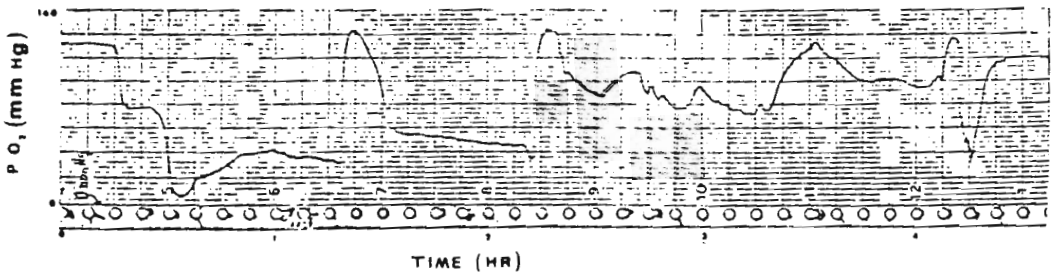

Fig. 5. Record of PO_2 in the head shaft of a glass tube inhabited by *Glycera dibranchiata*. Incurrent PO_2 = 160 mm Hg. Temperature 14°C.

The animal experiences wildly unstable oxygen conditions, although they are predictably unstable. Microenvironmental oxygen levels

are not especially low, however; at high tide when the ventilatory stream in unimpaired, oxygen in the microhabitat is high enough to permit functioning of bloodworm hemoglobin in gas transport. External PO_2 falls to levels where bloodworm hemoglobin operates as an oxygen reservoir only during the resting phase at high tide and then of course at low tide when the worm cannot ventilate (Mangum and Carhart, 1972).

When PO_2 changes are recorded in a closed container, a similar rhythmicity appears. Therefore, derivatives of the trace yield a simple, direct measurement of active and resting levels of aerobic metabolism at different oxygen concentrations. Identification of the two phases of oxygen uptake can be confirmed by making independent recordings of the product of activity, which is fluid flow (Mangum and Sassaman, 1969; Hoffmann and Mangum, 1970). In some annelids, aerobic respiration shuts down at a PO_2 well above zero and a switchover to anaerobic pathways presumably occurs. This phenomenon has also been encountered in some twenty-three species representing seven animal phyla (Prasada Rao and Ganapati, 1968; Mangum, 1970; Kushins and Mangum, 1971; Sassaman and Mangum, 1972; Mangum and Van Winkle, 1973), and it is not ordinarily a premonition of death. Many species live for days after it occurs. We are naturally intrigued by the question as to why the switch occurs, in the adaptive sense, when oxygen remains for the taking. An obvious answer might be that it happens when production of the ventilatory stream is no longer economical, i.e., in modern economic terms, when the marginal cost of the product equals the marginal revenue gained, or when the volume of oxygen that can be extracted from the ventilatory stream falls below that expended by the animal in generating the current. Testing this hypothesis in rigorous econometric fashion would be extraordinarily difficult because it rests on the projection of variable costs per production unit (Samuelson, 1955), or the measurement of different levels of metabolic and muscular activity at low PO_2's near the aerobic shutdown point where it is hard enough to distinguish active from resting metabolism. But we can project fixed costs or resting metabolism, and average costs of the activity at different oxygen levels. Under well-oxygenated conditions, the muscular activity involved in a ventilatory burst requires a four- to sevenfold metabolic increase in the terebellid polychaete *Amphitrite ornata*, a three- to fourfold increase in the onuphid *Diopatra cuprea*, and a two- to tenfold increase in the bloodworm *Glycera dibranchiata*, depending on the temperature (Coyer and Mangum, 1973). At lower PO_2's, the increase in aerobic respiration is reduced, but contributions from anaerobic pathways still cannot be evaluated.

Under well-oxygenated conditions, the oxygen extraction rate in the onuphid polychaete *Diopatra cuprea* is among the lowest known in animals with muscular mechanisms of ventilation. The water current in this species is exceptional in that it plays an important role in the biology of feeding (Mangum, Santos, and Rhodes, 1968). The current carries chemical stimuli which, if they consist of

suprathreshold concentrations of a glycoprotein or any one of several amino acids, elicit a complex response that culminates in ingestion (Mangum and Cox, 1971). The rate-determining requirement is therefore nutritional and not respiratory, a fairly unusual feature among animals with muscular ventilation. But at low oxygen concentrations the volume of flow and, thus, of oxygen available at the gills declines precipitously until it is only slightly higher than and not significantly different from the volume expended in the activity of procuring it. In Figure 6, the volume of oxygen available at each of three concentrations of environmental oxygen was computed from estimates of flow made by Dales, Mangum, and Tichy (1970), and the level of active metabolism was measured as described by Mangum and Sassaman (1969). We believe that the proximity of the intersect of these two curves to the shaded area of the abscissa, which spans the region in which aerobic shutdown occurs, is more than coincidence

Fig. 6. The cost of ventilation in *Diopatra cuprea*. Circles (●) indicate oxygen consumption in 1.5 gm worm and triangles (△) show volume of oxygen in incurrent ventilatory stream as a function of oxygen concentration at 17°C. Shaded area spans range of oxygen concentration at which aerobic shutdown occurs. Vertical bars represent standard error.
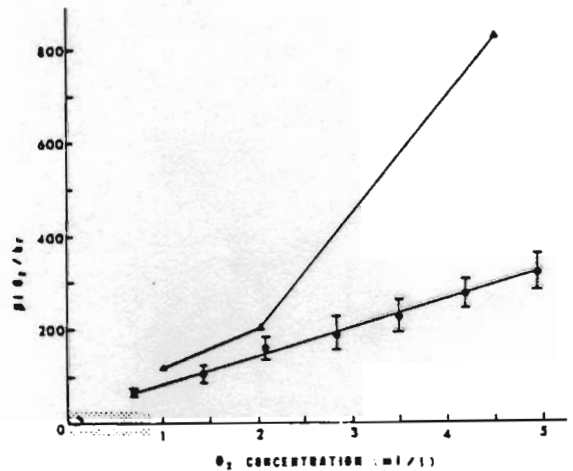
The argument is formulated in terms of understanding the adaptive significance of aerobic shutdown; its form is therefore teleological and not causal. At present we have no insight into the nature and operation of the switch. The adaptive importance of the response, however, is emphasized by evidence that it does not occur at a series of temperatures lower than 17.5°C, where production costs are reduced and revenue, or oxygen content, is enhanced (Mangum, 1972). One might suppose that the response would be similarly contingent upon body size, but within a species flow rate is not related in a systematic way to a relatively small range of body weights. Values of the correlation coefficient r for linear and logarithmic regression lines describing the relationship of these two variables (Dales, Mangum, and Tichy, 1970) are not significant ($P > .05$). While the correlation should certainly be tested over a wider range of body size, it is not apparent that the expression of flow rates in body size units would be a useful addition.

In contrast, oxygen extraction in the terebellid polychaete *Amphitrite ornata* is more typical of animals making currents by

muscular activity. The data in Figure 7 were estimated from integrals of continuous in situ measurements with the PO₂ microelectrode positioned in the head shafts of natural tubes. The shape of that curve, interestingly enough, resembles the shape of a curve describing the quantitative participation of the animal's hemoglobin in aerobic respiration at the same temperature (Mangum, unpublished data). Figure 7B shows the volume expended in active and resting metabolism down to an oxygen concentration where the two cannot be distinguished, and the volume of oxygen available as computed from the data in Figure 7A. Alternatively, if we compute the volume of oxygen available from flow measurements (Coyer and Mangum, 1973), the result is lower but not significantly so. In any event, the curve in Figure 7B describing the rate of decline of procured oxygen has a different shape from that in *D. cuprea*, and it predicts a net profit in oxygen essentially down to anoxia. In fact, we have never encountered the phenomenon of aerobic shutdown in *A. ornata*, regardless of temperature, and we know that the worm continues to engage

Fig. 7A. The fractional extraction or utilization by *Amphitrite ornata* of oxygen available in the incurrent ventilatory stream at 20°C and 31 o/oo. Vertical bars represent standard error.
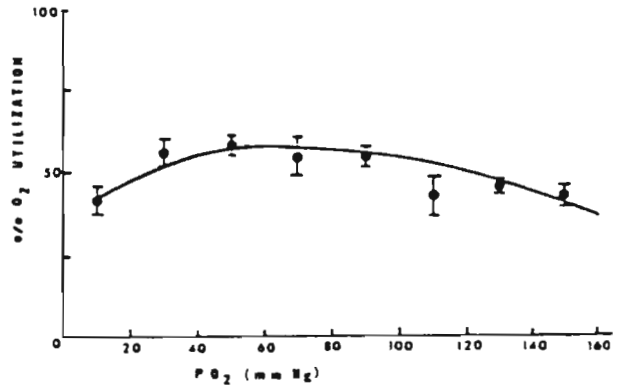

Fig. 7B. The cost of ventilation in a 3.37 gm *Amphitrite ornata* at 20°C. Oxygen consumption indicated during active (●) and resting (o) phases of the rhythmic ventilation cycle as a function of oxygen concentration. Closed squares (■) are used where the two can no longer be distinguished. Triangles (△) show volume of oxygen entering the animal, computed from data in 7A. Open square (□) shows volume of oxygen in ventilatory stream, computed from flow rates (Coyer and Mangum, 1973). Vertical bars represent standard error.
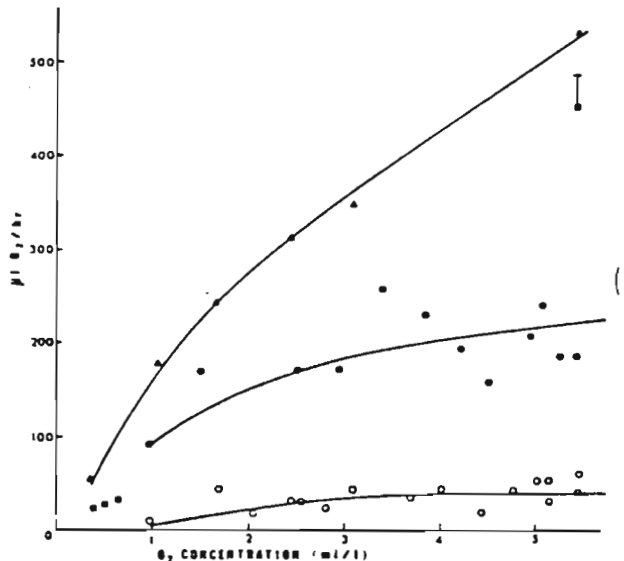
in bursts of muscular ventilation at external PO_2's lower than 10 mm Hg. At least in these two examples then, the phenomenon of aerobic shutdown seems to have a rational basis in respiratory economy.

REGULATION OF OXYGEN EXTRACTION

At a constant PO_2, changes in oxygen extraction rates such as those observed in animals generating ciliary currents (Fig. 1) may be due to alterations in fluid flow either inside or outside the gill, or changes of either term in the expression $\dot{V}_w/\dot{Q}$ for the ventilation: perfusion ratio, although we would be reluctant to assign it a numerical value for the reasons discussed below. Similarly, when the external PO_2 is reduced, the failure of oxygen extraction rates to reflect this reduction precisely constitutes evidence for a compensatory response. Low oxygen compensation may be affected by increased ventilation and/or circulation, or it may be due to enhanced transport of oxygen by a respiratory pigment. While a compensatory response in oxygen extraction by a vertebrate is usually explained solely in terms of fluid flow, there is some evidence that in the terebellid polychaete *Amphitrite ornata* it is partly attributable to the mode in which its hemoglobin operates (Mangum, unpublished data). Here, as in most invertebrates, our knowledge of circulatory dynamics is so primitive that we cannot assess the relative importance of gill perfusion and hemoglobin oxygenation. But we can evaluate the changes under low oxygen conditions in (1) ventilation or (2) both gill perfusion and hemoglobin oxygenation. When measurements of the volume of water pumped through the tube were made according to the procedure described by Dales, Mangum, and Tichy (1970), variation between the eleven individuals studied was so great that changes would be obscured by presenting the results in absolute values. When the data are analyzed as paired observations, however, it is clear that an initial reduction in the environmental oxygen level to 3.1 ml/l brings about a transient increase in flow of about 25% over the control value (Fig. 7B). This response, achieved by an increase in the amplitude of muscular movements rather than a change in parameters of the spontaneous rhythm itself, persists for only a few hours and then it diminishes until the rate is indistinguishable from the control. Further reductions to 1.9, 1.1, and 0.5 ml/l cause no further changes, although one of the eleven worms did attempt to emerge from its tube under essentially anoxic conditions. There is no mechanism increasing the ventilatory rate at low oxygen levels. Therefore, the failure of oxygen uptake and extraction to show a linear decline in the face of a decreasing PO_2 gradient across the gills (Mangum, unpublished data) as well as a decreasing volume of oxygen available (Fig. 7B) implicates a compensatory response by the circulatory system.

Flow across the gills of lamellibranch molluscs has often been computed from the clearance rate of small particles in suspension (Jørgensen, 1966). The method probably yields highly unrealistic values due to incomplete particle retention. When *Mya arenaria* and *Rangia cuneata* are allowed to clear prodag (Anderson, 1972) at air saturation, the estimates of flow (vol/time) are an order of magnitude lower than those required to explain the oxygen uptake and oxygen extraction figures. In contrast, the estimates made volumetrically for *A. ornata* (Fig. 7B) are not significantly lower than those required to explain oxygen uptake and oxygen extraction.

If we assume that particle retention is not oxygen-dependent, however, the response of clearance rate to low oxygen levels may permit identification of the compensatory system. In *M. arenaria*, the estimated rate at PO_2 = 140 mm Hg is 344 ± 32 (N = 11) ml/hr, and at PO_2 = 30 mm Hg it is only 15% of that value, or 52 ± 2 (N = 7) ml/hr. In *R. cuneata*, the rates are 68 ± 9 (N = 5) ml/hr at PO_2 = 105 mm Hg, and 7 ± 0 (N = 10) ml/hr at PO_2 = 28 mm Hg. In both species the clearance rate varies directly with PO_2, while the oxygen extraction rate varies inversely (Figs. 2A and 3B). This result suggests that the compensatory responses enabling the clams to maintain a relatively stable rate of oxygen uptake (Figs. 2C and 3A) occur within the gill, a conclusion that also has been reached from different kinds of evidence for the mussel *Mytilus edulis* (Bayne, 1971).

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