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THE RESPIRATION OF *PTEROIDES GRISEUM* (BOHADSCH) A PENNATULID COELENTERATE

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It has been shown that the oxygen consumptions of various anthozoans are generally comparable with those of other invertebrates if the dry weights rather than the wet weights are considered (Brafield & Chapman, 1965). We have also suggested that the endoderm is probably the major site of oxygen uptake in pennatulids, associated with water movements into and out of the enteron. Three main sources of evidence support this view. First, the enteric water has a low oxygen concentration. Secondly, a fully contracted specimen consumes oxygen at a low rate, possibly due to a severely limited enteric circulation. Thirdly, measurements of the oxygen concentration of the water around a specimen in a closed vessel are sometimes inconsistent. Such variations might well be partly due to fairly regular movements of water in and out of the enteron, the inconsistent estimations having been made either just before or after an efflux of relatively deoxygenated enteric water. This source of inaccuracy in measuring consumptions can be avoided only if the oxygen concentration is measured continuously. Consequently experiments have been conducted in which a continuous-flow respirometer was used in an attempt to demonstrate whether a rhythmic enteric irrigation does occur in pennatulids; for if it does, and water which has become partly deoxygenated by oxygen uptake through the endoderm is periodically expelled from the enteron, a continuous record of the oxygen concentration of water which has been flowing slowly past the animal should show a rhythmic rise and fall. *Pteroides griseum* was used in these experiments because this species has a spacious enteron, and because a good supply of large specimens was available.

To obtain a continuous record of the oxygen concentration of the water passing a specimen the latter was placed in a glass tube 25 cm. long and 5 cm. in diameter (Fig. 1, *H*). Guard wires prevented the animal blocking the entrance and exit tubes (*G* in Fig. 1). A regular flow of water was achieved by maintaining a constant head of water at *A*—the aspirator *B* was kept completely full by dripping water into it at a greater rate than the drip rate at the effluent capillary *L*. The flow rate could be finely controlled by adjusting the height of this capillary. Flow rates were measured by collecting the effluent water in a measuring cylinder or by counting the drops falling from *L* in unit time. The flow rate was varied according to the size of the animal, but was rarely less than 2 or greater than 4 ml. per minute. The water in *B* was kept saturated with air by pumping air through the diffuser block *C*. A constant temperature of 20° C., measured by a thermometer (*D*) in the respiration chamber, was maintained throughout by enclosing the apparatus in a water bath.

The oxygen concentration of the water was measured at *J* (Fig. 1). By manipulating

screw clips the water under test was drawn either from the respiration chamber or directly from the aspirator (by way of the bypass *F*). In this way either the oxygen concentration of the water entering or that of the water leaving the respiration chamber could be determined, and knowing the flow rate the oxygen consumption of the animal could be calculated. The oxygen concentration was measured continuously by means of a Beckman 777 Oxygen Analyzer, which employs an enclosed solid electrode system as a polarographic sensor (*I* in Fig. 1). A thermistor enclosed in the sensor provides temperature compensation. At slow rates of flow the water around the sensor must be stirred, and this was done continuously by means of a magnetic stirrer (*K*). The motor was connected through a variable resistance, which allowed a range of speeds to be used. A continuous record of the oxygen concentration was obtained by linking the Analyzer through a specially constructed amplifier to a strip-chart recorder.

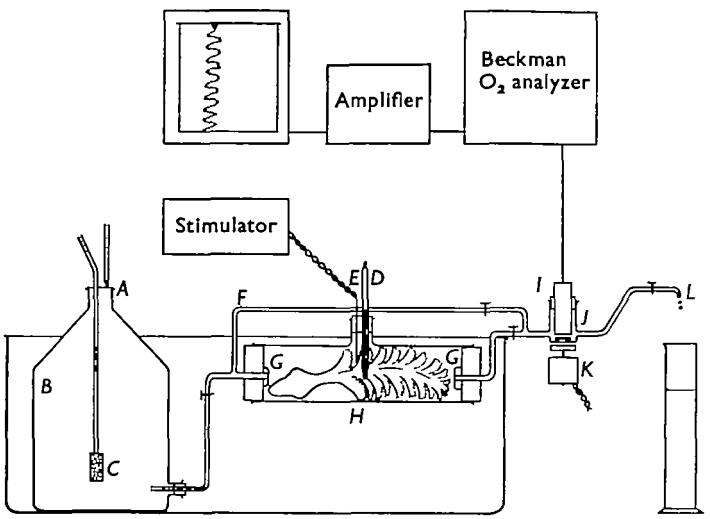

Fig. 1. Apparatus used to determine the oxygen consumption of *Pteroides griseum*. See text for further details and explanation of lettering.

A complete and rapid contraction of the specimen could be induced by lowering an electrode (*E* in Fig. 1) into the respiration chamber until it touched the specimen and stimulating the animal electrically. A suitable stimulation was usually found to be a 2 sec. burst of 10 V. impulses, the impulses occurring at 100 msec. intervals. It was established that these impulses did not themselves measurably alter the oxygen concentration of the water by control experiments in which they were passed when no specimen was present.

The traces obtained with the strip chart recorder, when monitoring the oxygen concentration of the water leaving the respiration chamber, could be divided into three categories. First, 'horizontal' straight line traces were occasionally obtained, reflecting a constant oxygen consumption by the animal. Secondly, an oscillation in the record sometimes occurred, of rather variable wavelength and amplitude, which we consider to be caused by a rhythmic expulsion of relatively deoxygenated water from the enteron. Thirdly, records of large and abrupt falls in oxygen concentration were obtained, always immediately following complete and violent contrac-

tions of the specimen, whether these contractions were spontaneous or induced electrically.

A typical straight line trace is shown in Fig. 2. In this example the oxygen concentration of the water leaving the respiration chamber was 6·3 parts per million (p.p.m.) while that of the inflowing water was 7·2 p.p.m. The flow rate in this case was 100 drops per minute (one drop equalled 0·036 ml.) and the dry weight of the specimen was 0·792 g. From these data the oxygen consumption can be calculated and in this case equals 0·245 mg./g. dry wt./hr. Oxygen consumptions were calculated in this way for all straight line traces lasting more than an hour, of which there were ten, all similar in form to Fig. 2 and all having the inflowing water saturated with air.

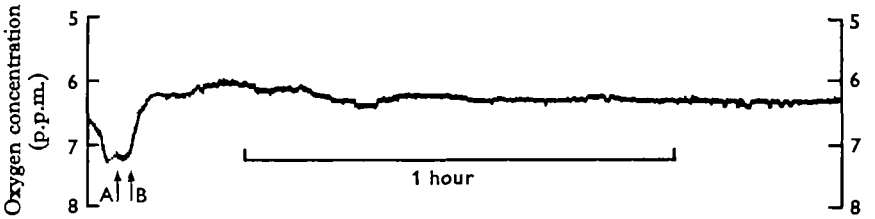

Fig. 2. A typical straight line trace, showing a constant rate of oxygen consumption by the specimen. Record reads from left to right. *A*, Inflow water; *B*, change to outflow water.

Table 1. *Oxygen consumptions calculated from straight line traces and ranked, among the two weight ranges, according to the degree of expansion of the specimens at the time the records were obtained*

Condition of specimen	Oxygen consumption (mg./g. dry wt./hr.)	Dry weight of specimen (g.)
Fully contracted	0·076	0·794
Fully contracted	0·203	0·747
Very contracted	0·241	0·747
Very contracted	0·245	0·792
Rather contracted	0·245	0·792
Rather contracted	0·272	0·794
Very expanded	0·289	0·747
Very contracted	0·150	1·870
Rather contracted	0·106	1·830
Rather contracted	0·165	1·830

Table 1 shows the extent of expansion, the oxygen consumption and the dry weight of the specimen for each of these ten records. It can be seen that the oxygen consumption increases with the degree of expansion of an animal, at least for the specimens of about 0·8 g. This is probably because both ectoderm and endoderm provide a larger surface area in more expanded specimens. In no case, however, was a straight line trace provided by a fully expanded animal, and eight of these ten records relate to animals which at the time were at least partly contracted. Records from fully expanded specimens were never of the straight line type, but showed fairly regular fluctuations instead.

Examples of this second main type of record, showing oscillations in the oxygen concentration of the water leaving the respiration chamber, are shown in Fig. 3. In all, ten traces fluctuating around the same oxygen level for more than 30 min. were obtained, and data from these ten are shown in Table 2. In every case the specimen

was fully expanded at the time the traces were made. The oxygen consumptions shown in Table 2 were obtained in a similar way to those derived from the straight line traces, except that in the case of these rhythmic records the oxygen concentrations at 2½ min. intervals over the period of each record were averaged and this mean concentration was used when calculating the oxygen consumption. The resulting ten con-

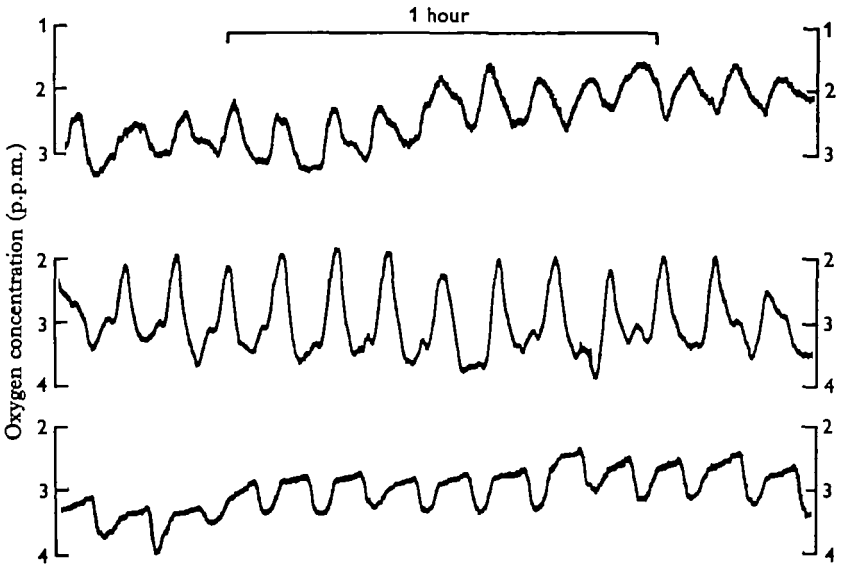

Fig. 3. Three examples of the rhythmic traces obtained with fully expanded specimens. Records read from left to right.

Table 2. *Analysis of the ten rhythmic traces which persisted around the same oxygen concentration for more than* 30 *minutes*

Dry weight of specimen (g.)	Oxygen consumption (mg./g./hr.)	Mean oxygen consumption	Duration of record (hr.)	Mean amplitude (p.p.m.)	Mean wave-length (min.)
0·792	0·78	—	5½	0·21	6·3
0·792	0·82	—	1	0·36	8·6
0·792	0·95	—	¾	0·20	5·6
0·792	1 23	0·95	1¼	0·30	7·5
1·870	0·41	—	1	0·64	13·3
1·870	0·44	—	2¼	0·62	6 1
1·870	0·47	—	4½	0·70	8·2
1·830	0·54	0·47	1¾	0 39	7·0
5·200	0·16	—	¾	0·44	5·6
5·200	0 22	0·19	2¼	0·55	5·9

sumption rates (Table 2, second column) are plotted against the dry weights of the specimens in Fig. 4, together with the ten from the straight line traces. There is clearly an exponential relationship between oxygen consumption and dry weight, similar to that characteristic of more advanced phyla. Of more interest are the markedly higher oxygen consumptions of fully expanded specimens (rhythmic traces) as compared with contracted animals (straight line traces). It seems reasonable that a contracted specimen, which is apparently not moving water in and out of the enteron, is

consuming oxygen almost solely through the ectoderm, whereas a fully expanded animal, irrigating the enteron, is consuming oxygen through the endoderm as well. Consequently the difference in total oxygen consumption between expanded and contracted specimens is some indication of endodermal oxygen consumption. To consider, for example, the values in Fig. 4 for the specimens of about 0·8 g., this difference equals 0·950 less 0·224, or 0·726 mg./g./hr. This rate of consumption is likely to be the endodermal contribution in expanded specimens, and is over three times the consumption rate of specimens respiring only through the ectoderm (0·224 mg./g./hr.). Thus in an animal which is rhythmically irrigating the enteron

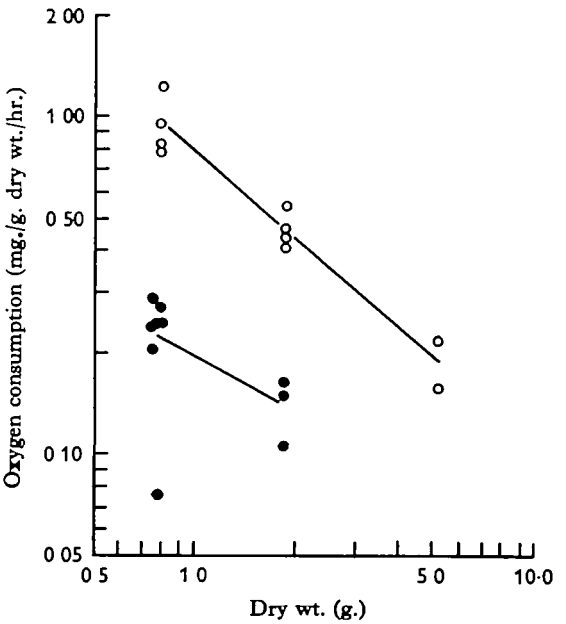

Fig. 4. The relation of oxygen consumption to dry weight of the specimen. Open circles, consumptions calculated from rhythmic traces (fully expanded specimens). Closed circles, consumptions calculated from straight line traces (contracted specimens). Logarithmic scales.

about three times as much oxygen may be entering through the endoderm as through the ectoderm, although the endoderm is not directly exposed to the environment. There are, of course, other considerations; for example, the ectodermal contribution to total oxygen consumption will increase in expanded animals because the surface area will be greater. And if fully expanded specimens are actively irrigating the enteron they will be expending more energy than contracted animals. Nevertheless, it is reasonable to assume that at a conservative estimate about two-thirds of the total oxygen consumed by an expanded specimen enters through the endoderm.

There seems little doubt that the rhythmic records (Fig. 3) result from periodic expulsions of some of the relatively deoxygenated water in the enteron. Each trough on a rhythmic trace represents a small amount of relatively deoxygenated enteric water passing the electrode. The amplitude of a fluctuating trace is consequently some indication of the quantity of enteric water eliminated at each pulse and the

extent of its deoxygenation relative to the water surrounding the animal. In Table 2 the column headed 'mean amplitude' shows the mean values for half the distance from trough to crest of all cycles within the period. It can be seen from this column that for an individual specimen the amplitude of the fluctuations is very consistent, though it varies fairly widely from animal to animal. The amplitude is not always greater in a larger specimen than a smaller one although the former's enteron will be more spacious. This may be because the oxygen concentration of the enteric water, as well as the amount of water eliminated, will affect the trace amplitude.

The final column of Table 2 shows for each record the mean of all wavelengths within the period, a wavelength being the distance between two adjacent peaks in the rhythmic trace. The average of these ten means is 7·4 min., which would suggest that a pulse of enteric water is generally eliminated every 7–8 min. This is of interest because usually when an expanded specimen of *Pteroides* is observed carefully small constrictions can be seen to progress along the body, passing a given point at about 8 min. intervals. Each of these constrictions, or 'peristaltic waves', appears as a fairly deep ring-like depression around the animal, moving slowly and steadily either from peduncle to rachis or in the reverse direction, though at any given moment the two or three constrictions visible in a particular specimen are moving in the same direction as one another. As these peristaltic waves occur at about the same time interval as the fluctuations in the rhythmic traces, i.e. about every 8 min., it seems extremely likely that the arrival of a peristaltic wave at the tip of the specimen causes a little water to be expressed from the enteron, and that it is these pulses of enteric water which cause the regular fluctuations in the traces. Presumably this water leaves either through the terminal polyps of the rachis or through the pores at the base of the peduncle, depending on the direction in which the waves are moving.

Attempts were made, using methylene blue and carmine, to establish where water enters and leaves the enteron, but unfortunately no firm conclusions could be drawn, possibly because the volume of water involved in each movement is so small and its speed of exit slight. Even when an expanded specimen was forced to contract completely and rapidly it was impossible to be sure whether the enteric water left primarily through the polyps, the siphonozoids, or the apical peduncular pores. Musgrave (1910) also failed to obtain a clear concept of the routes of water movements in *Pteroides griseum* and *Pennatula* spp. Her experiments with methylene blue suggested that water could enter or leave the enteron by way of either the peduncular pores or the polyps. Parker (1920) concluded that water enters the pennatulid *Renilla* sp. through the lateral siphonozoids. Mori (1960) recorded mechanically the degree of expansion of *Cavernularia obesa*. This pennatulid is generally expanded at night and contracted during the day, but Mori's records of expanded specimens also show small variations in size occurring at about ten minute intervals. Though not commented upon by Mori these small fluctuations might bear some relation to the peristaltic waves we have observed in *Pteroides*. No other short-term regular volume changes or waves of contraction appear to have been reported, although various natural rhythms have been observed in the pennatulid *Veretillum cynomorium* (Ceccatty, Buisson & Gargoüil, 1963).

Finally, having considered the straight-line traces and the rhythmic records, the third group of results may be briefly considered. These show a rapid and marked fall

in the oxygen concentration of water passing the electrode immediately after a sudden and complete contraction of the expanded specimen (Fig. 5), whether these contractions were natural or electrically induced. The fact that a rapid and extensive reduction in the volume of the enteron is accompanied by a dramatic fall in the oxygen concentration of the water surrounding the animal provides further evidence that the enteron contains relatively deoxygenated water. It is quite clear, therefore, that an extensive consumption of oxygen occurs through the endoderm, and that enteric water is generally replaced in expanded specimens by a rhythmic irrigation process. Whether these regular irrigation movements are primarily concerned with respiration or also associated with feeding is unknown.

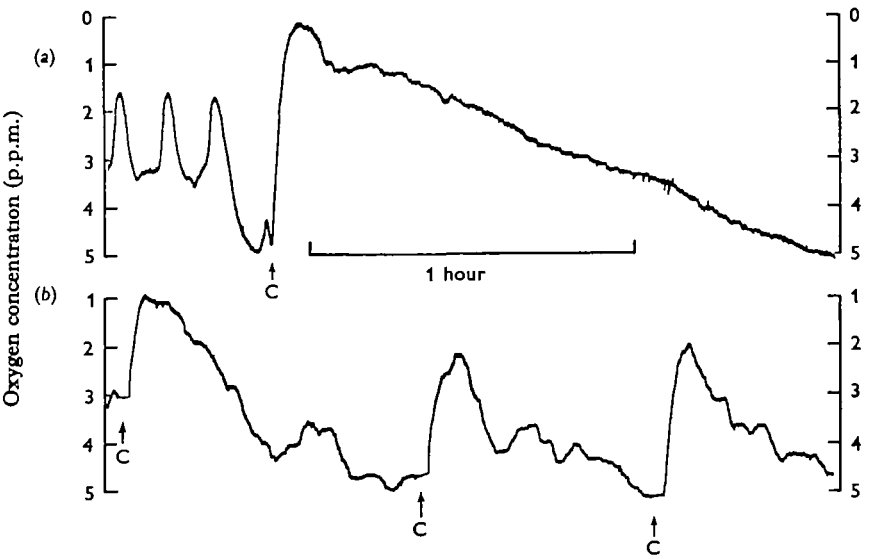

Fig. 5. Examples of the rapid decline in outflow oxygen concentration immediately following a complete and rapid contraction of a fully expanded specimen. C, time of contraction. Records read from left to right. (*a*) Natural contraction; (*b*) electrically stimulated contractions.

SUMMARY

1. The respiration of the pennatulid *Pteroides griseum* has been investigated by means of a continuous-flow polarographic respirometer and a strip-chart recorder.

2. The rate of oxygen consumption bears the same exponential relation to body weight as in more advanced phyla, and is markedly greater in expanded specimens than in contracted ones.

3. It is suggested that contracted specimens consume oxygen almost exclusively through the ectoderm but that in expanded specimens at least two-thirds of the total oxygen consumed enters through the endoderm.

4. Several sources of evidence confirm that the water within the enteron is poorly oxygenated. Rhythmically fluctuating records of the oxygen concentration of water which has flowed past expanded specimens are the result of periodic expulsions of some of this relatively deoxygenated enteric water.

5. The irrigation of the enteron is very probably brought about by peristaltic waves of contraction which pass along the length of the animal.

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