

OXYGEN CONSUMPTION BY THE SEA ANEMONE *CALLIACTIS PARASITICA* (COUCH)

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SUMMARY

Oxygen consumption by *Calliactis parasitica*, measured in a continuous-flow polarographic respirometer, yielded a slope of 0.92 when plotted against body weight on log scales. This high value is discussed in terms of the sea anemone's basically laminate nature. Strip-chart records of the oxygen concentration of water which had just passed a specimen of *Calliactis* commonly showed rhythmic fluctuations, either of low amplitude and high frequency or high amplitude and low frequency (mean cycle lengths 11 and 34 min respectively). The fluctuations are explained in terms of rhythmic muscular contractions which irrigate the enteron for respiratory purposes. Analysis of the slow fluctuations indicates that the endoderm is responsible for about 18% of the total oxygen consumption.

The oxygen concentration of water in the enteron, measured and recorded continuously, was 4-27% of the air-saturation level. These strip chart records also frequently showed rhythmic fluctuations (mean cycle length 12 min), apparently resulting from the muscular contractions.

INTRODUCTION

The physiology of anthozoans is poorly understood in comparison to their anatomy, which appears to be the most complex to be found among the coelenterates or other animals built on a basically laminate body plan. Studies of the respiration of anthozoans have shown that the endoderm, the major part of the total surface area, can be an important site at which oxygen is taken up. In some species the oxygen supply to the endoderm is apparently regularly replenished by irrigation of the enteron (Brafield & Chapman, 1967; Brafield, 1969; Jones, Pickthall & Nesbitt, 1977), by means of the periodic muscular contractions which occur widely in the group.

In this paper the respiration of *Calliactis* is studied by means of continuous-flow respirometry and continuous measurement of the oxygen concentration in the enteron. Continuous-flow respirometry aids study of changes in respiratory rate and does not involve changes in ambient concentration. This technique has been used in only a few studies of anthozoan respiration (Brafield & Chapman, 1967; Chapman, 1972; Shumway, 1978) and was not used in the previous study of *Calliactis* (Brafield & Chapman, 1965).

The neuromuscular system of *Calliactis* is probably better understood than that

of any other coelenterate, through the work of Pantin (1935), Chapman (1947), Needler & Ross (1958), Ewer (1960), Shelton (1975), Lawn (1976*a* and *b*) and the series of papers in this journal by McFarlane and his co-workers. The experiments described here can therefore be set against a good background knowledge of the animal's behaviour and neuromuscular physiology.

MATERIALS AND METHODS

Specimens of *Calliactis* were obtained from Plymouth and kept in running sea water in a 10 °C aquarium room for 2–3 weeks before use in experiments. They were fed every 5 days with fragments of fish muscle, except just before and during an experiment.

Oxygen uptake by the whole animal was measured by a continuous-flow method similar to that used by Brafield & Chapman (1967) for pennatulids and by Brafield (1968) for an echiuroid, but with a peristaltic pump to maintain constant flow (Brafield & Matthiessen, 1976). Aerated sea water from a 20 l aspirator was drawn at a constant rate (600–800 ml/h, depending on the size of the specimen) through a respiration chamber containing the sea anemone. This chamber was of Perspex, in the form of a cylinder 12 cm high and 10 cm in diameter, with removable base plate and lid. The water entry tube in the lid, and the exit tube near the base, could be inserted in a number of positions, in order to provide optimal flow across the specimen. To minimize disturbance, animals were transferred to the chamber on the ground-glass plates on which they had settled in the aquarium. Experiments were carried out at 10 °C in a constant-temperature room. Oxygen concentration was measured with a Beckman Oxygen Analyzer and recorded on a strip-chart recorder. The oxygen electrode was placed in a small vessel through which the water flowed soon after leaving the respiration chamber. Water passing the electrode was continuously stirred by a magnetic stirrer. The oxygen concentration of water entering the chamber could be monitored by opening a by-pass around the chamber. The volume of water in the respiration chamber and the difference between the inhalant and exhalant oxygen concentrations were small enough to make the corrections for lag devised by Evans (1972) and Niimi (1978) unnecessary.

The oxygen concentration in the enteron was measured continuously with a miniaturized oxygen electrode produced by Searle Medical Products (Soutter, Conway & Parker, 1975). Animals were placed in glass troughs of aerated sea water slowly stirred with a magnetic stirrer. The temperature was 18 °C. Insertion of the electrode, which is long (500 mm), thin (1.7 mm) and flexible, caused no apparent response from the sea anemone. In the absence of such an electrode, previous measurements of enteric oxygen content have required the removal of water samples. Preliminary tests in small enclosed volumes of water confirmed that the electrode consumed insufficient oxygen to affect the results. The probe was either inserted well into the enteron or placed just by or in the mouth. It was twitched occasionally to ensure that it was not embedded in acontia or mesenteries.

RESULTS

The mean rates of overall oxygen consumption for the four specimens from which the most exhaustive and consistent records were obtained were 474, 588, 661 and

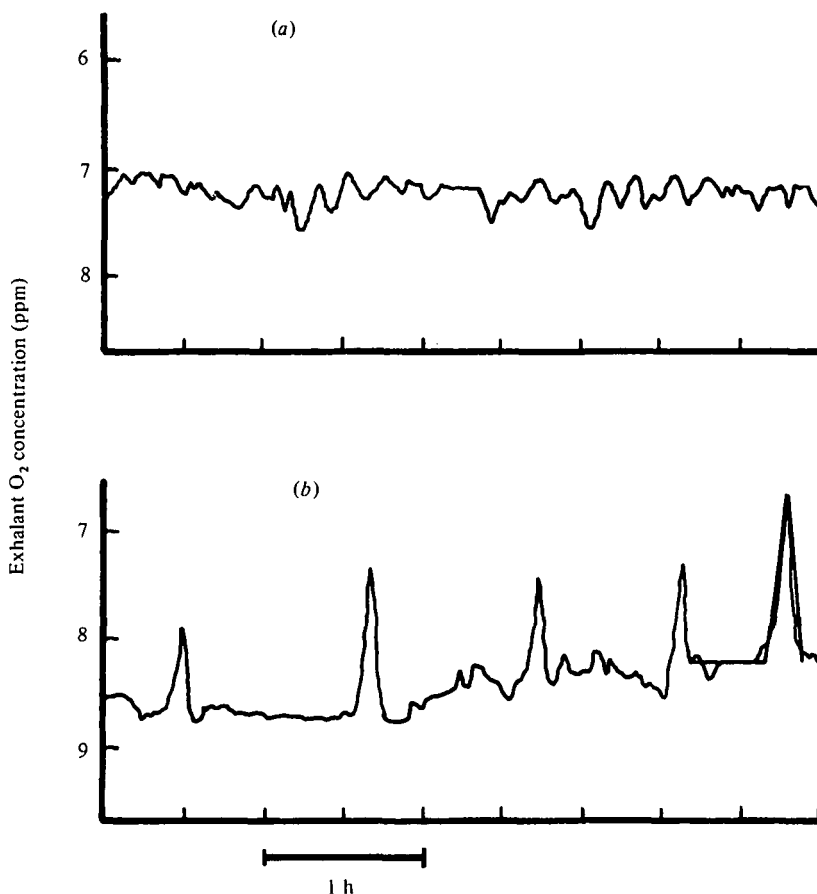


Fig. 1. Strip-chart records of the oxygen concentration of water that has just passed a specimen of *Calliactis* in the continuous-flow respirometer, showing (a) small fluctuations, (b) less-frequent and more pronounced fluctuations. The last cycle is overdrawn in the idealized fashion used in calculating the ectodermal and endodermal contributions to total oxygen consumption (see text).

953 $\mu\text{g/h}$, for body dry weights of 1.306, 1.752, 2.142 and 2.700 g, respectively. Plotted on log scales these values give a straight line ($r = 0.97$) with a slope of 0.923.

The strip-chart records from most specimens sometimes remained steady for up to about 5 h, but the records also showed two types of regular fluctuation. First, there were times when an abrupt and pronounced fall in oxygen concentration was recorded, with a subsequent rise to the original level (Fig. 1 b). Such fluctuations had a mean cycle length of 33.7 min (Fig. 2). They were seen to coincide with marked contractions of the animal and thus appear to represent expulsions of deoxygenated water from the enteron. Secondly, there were small but frequent fluctuations in the records (Fig. 1 a), with a mean cycle length of 10.6 min (Fig. 2), suggesting a more frequent expulsion of smaller amounts of water.

Overdrawn on the right of Fig. 1(b) is the part of a record taken to be one cycle. The ectodermal contribution to the oxygen consumed during a cycle is reflected in the level and duration of the horizontal part, whereas consumption by the endoderm is

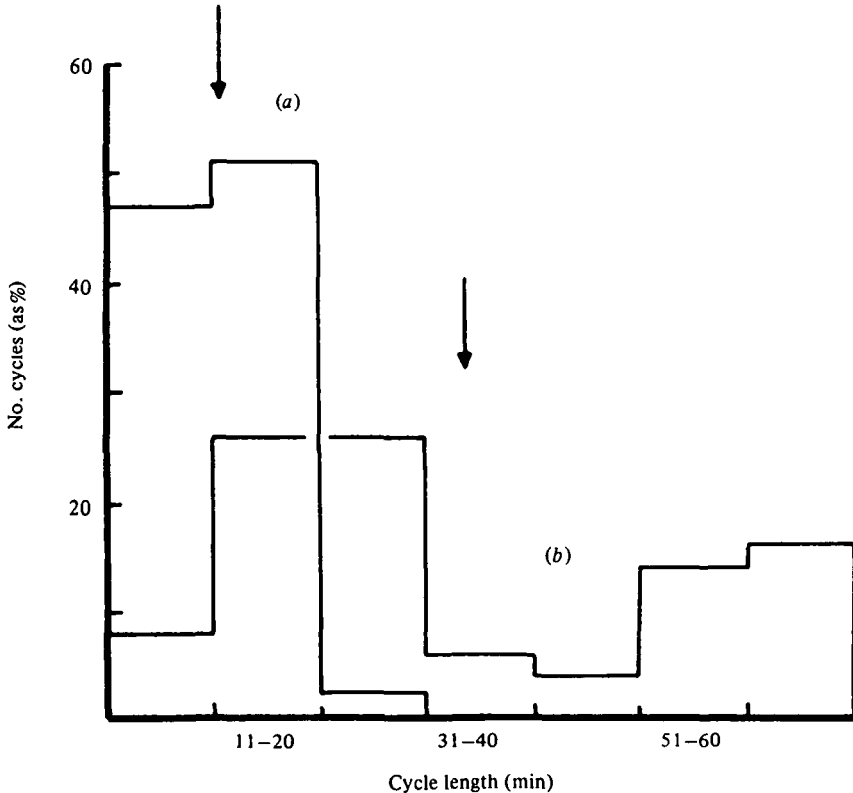


Fig. 2. (a) The variation in cycle length of 174 small fluctuations in oxygen concentration such as those of Fig. 1 (a), grouped into 10-min bands and expressed as percentages. (b) Similarly for 50 of the more marked fluctuations of the type shown in Fig. 1 (b). Mean cycle lengths (indicated by arrows) are 10.6 and 33.7 min for (a) and (b) respectively.

related to the area of the triangle which represents the abrupt fall and rise in oxygen concentration at the expulsion of enteric water. From such basic measurements, the ectodermal and endodermal contributions to total oxygen consumption were calculated for 10 cycles from one specimen and 5 from a second. The mean endodermal contribution as a percentage of the total oxygen consumption was 18.7% (standard error ± 1.86) for the first specimen and 17.2% (S.E. ± 2.21) for the second.

Enteric oxygen concentrations varied widely, between 4 and 27% of the air-saturation level. Rhythmic fluctuations were a feature of almost all these records (Fig. 3). The lengths of 90 such cycles were measured, from a total of 20 h recording from six specimens. They were grouped into 2 min bands (Fig. 4) and their mean is 12.4 min. Although cycle lengths varied widely, variability in the short-term was generally small for a given specimen. When the probe was placed at or just inside the mouth the records showed less clear fluctuations in oxygen concentration. Where discernible, however, they were shorter (mean 6.8 min), as seen in Fig. 4.

DISCUSSION

Plotting overall oxygen uptake against body weight on log scales gave a line with slope of 0.92, higher than the value of 0.75 typical of metazoan poikilotherms other

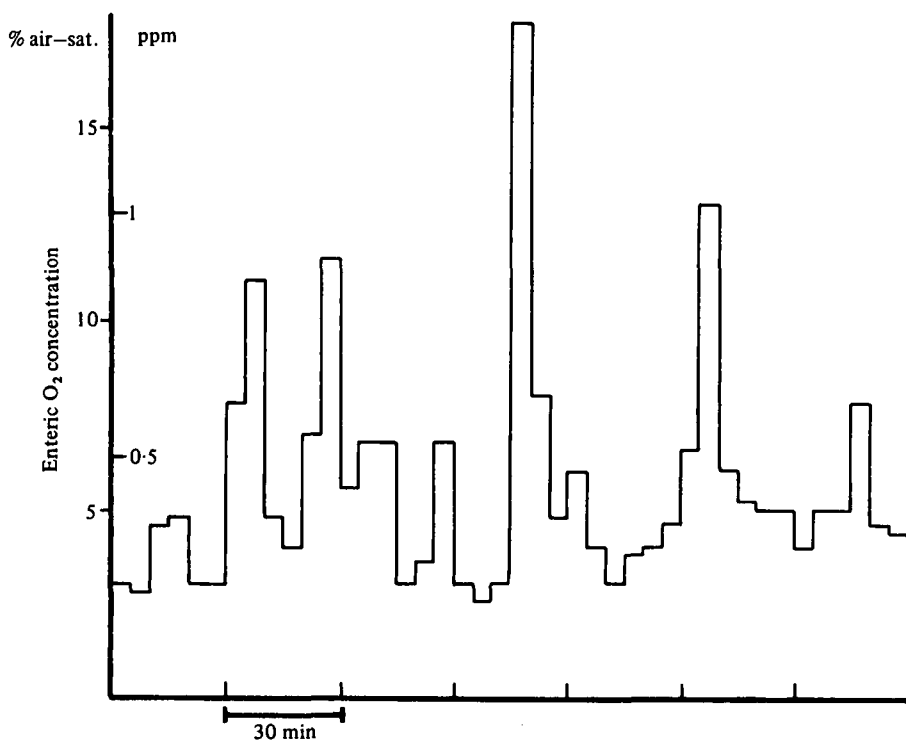


Fig. 3. Histogram drawn from part of a typical strip-chart record of the oxygen concentration of the water in the enteron of *Calliactis*, showing the mean value for each 5 min period.

than the very smallest (Hemmingsen, 1960). A slope of about 1 could be obtained if the volume or weight of tissue doubled as surface area doubled. This could be expected in anthozoans, which are built on a basically laminate plan. Similar high values have been found for some other anthozoans: 0.89 for *Metridium senile* (Shumway, 1978) and 0.834 for *Anthopleura elegantissima* (Shick *et al.* 1979). However, low values have also been found: 0.539 for *Metridium* (Shick *et al.* 1979) and 0.652 as a pooled value for *Metridium*, *Diadumene leucolena* and *Haliplanella luciae* (Sassaman & Mangum, 1970). Clearly other factors are relevant, such as the proportion of the total surface area actually involved in oxygen uptake, but at least in some cases high values for the slope may be a result of the basically laminate form of these animals. The relation between oxygen consumption and body weight of anthozoans will be fully explored in a later paper, and work is in hand on the rate of diffusion of oxygen across the mesogloea of *Calliactis*, which is relevant to the extent to which the ectodermal and endodermal layers may take up oxygen from the water bathing them.

The endodermal contribution to total oxygen consumption was found to be about 17–19%. This compares well with the 11–50% ('1/2 to 1/9') deduced by Jones *et al.* (1977) for *Metridium*, but falls short of the 66% or so found by Brafield & Chapman (1967) for *Pteroides griseum*. In the pennatulid, however, there is a one-way flow of water through the colony, maintained by peristalsis (Brafield, 1969), and perhaps this is a more efficient irrigation system than that of sea anemones. The values for

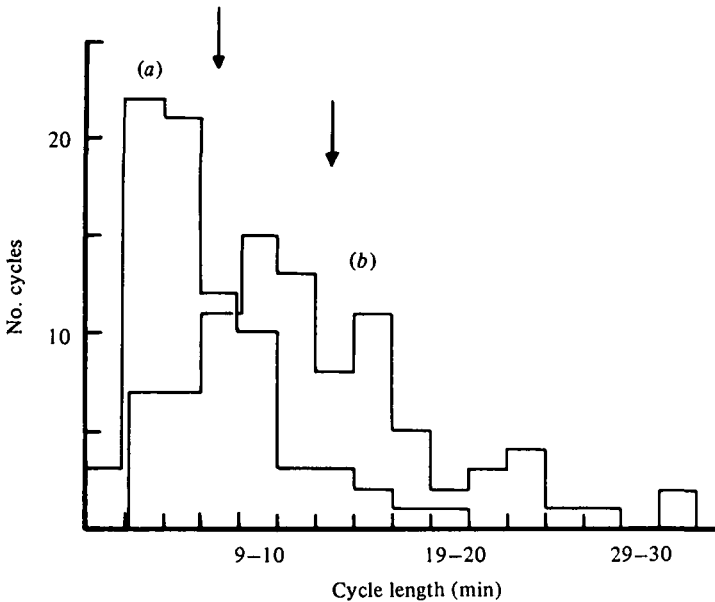


Fig. 4. (a) The variation in cycle length of 78 fluctuations in oxygen concentration obtained with the oxygen electrode at or just inside the mouth of *Calliactis*, grouped into 2-min bands. (b) Similarly for 90 fluctuations obtained with the electrode well inside the enteron. Mean cycle lengths (indicated by arrows) are 6.8 and 12.4 min for (a) and (b) respectively.

Calliactis and *Metridium* are substantial, however, and support the suggestion that rhythmic enteric irrigation supplies oxygen to the endoderm.

The enteric oxygen concentrations found, 4–27% of the air-saturation level, are lower than those reported for other anthozoans. Brafield & Chapman (1965) slit pennatulids lengthwise to obtain samples of enteric fluid, finding oxygen concentrations of 45% of the air-saturation level for *Pennatula rubra* and 26% and 60% for two specimens of *Pteroides griseum*. From samples of enteric water withdrawn with a syringe, Sassaman & Mangum (1972) found oxygen concentrations equivalent to 36% of ambient for *Metridium senile* and 41% for *Haloclava producta*. Similarly, Sassaman & Mangum (1974) found an enteric water P_{O_2} equivalent to about 25% of ambient in *Ceriantheopsis americanus*. Taking samples of enteric water for oxygen analysis is not very satisfactory, however, because it is discontinuous. The variation in the values above is probably due partly to real differences between species and partly to variation in other factors such as temperature. Such variation might also result, however, from samples being unwittingly taken at different points during cyclic fluctuations in enteric oxygen concentration (of the kind found by the continuous monitoring method used in the present work).

The rhythmic oxygen records described here correspond closely with observations of the movements of *Calliactis* (Needler & Ross, 1958; present study). First, the mean cycle length for the smaller but more frequent fluctuations in the respirometer records is 11 min (Fig. 2) and that of records from the probe inserted in the enteron 12 min (Fig. 4). Needler & Ross recorded contractions of the marginal and sub-marginal regions, accompanied by column shortening and disc depression, at 10–15 min intervals; and film records gave a mean cycle length of 13 min for the marginal

movements of an 'active' animal (111 per 24 h). This close correspondence in the timing of respiratory and behavioural events supports the conjecture of Needler & Ross that such movements 'are probably carrying out minor pumping and circulating activities'. Secondly, the larger but less-frequent fluctuations in the oxygen record have a mean cycle length of 34 min (Fig. 2), and Needler & Ross found closures or partial closures to have a mean period of 41 min (35 per 24 h). Again the correspondence is close, and the contractions mentioned above which were seen by me to accompany such abrupt changes in the oxygen concentration surely correspond with the 'closures or partial closures' of Needler & Ross, who thought these larger movements 'could provide for an exchange of water on a bigger scale'. Furthermore, these authors noted that the margin of *Calliactis* is 'frequently' thrown into folds by local contractions. Perhaps these cause the rapid fluctuations found when the Searle probe was placed at or near the mouth (mean cycle length about 7 min, Fig. 4). Although there is great variation between individuals, and in the same individual at different times, it seems certain that two types of periodic contractions (moderate ones at about 10–15 min intervals and much more pronounced ones at about 35–40 min intervals) serve to irrigate the enteron to correspondingly varying extents, causing either modest or considerable expulsions of deoxygenated water.

Respiratory rhythms have been found in other anthozoans; by Brafield & Chapman (1967) for *Pteroides griseum* (mean cycle length 7.4 min), by Chapman & Theodor (1969) for *Eunicella stricta* (cycle lengths 9–14 min), by Chapman (1972) for *Renilla köllikeri* (3–6 min), and by Jones *et al.* (1977) for *Metridium senile* (mean 28 min) and *Actinia equina* (24–40 min). These were linked with rhythmic movements in the cases of *Pteroides*, *Renilla* and *Metridium*. Buisson (1971) observed 'peristaltic waves and pulsations' in *Veretillum cynomorium*, and peristaltic waves irrigate the burrow of *Haloclava producta* (Sassaman & Mangum, 1972). So rhythmic movements are widespread among anthozoans, but their cycle length differs widely and it has not always been possible to link them with fluctuating oxygen concentrations.

The control mechanism of the irrigatory contractions of *Calliactis* is uncertain. They may be controlled endogenously, by neural mechanisms such as those described by McFarlane (1973*a, b*, 1974*a, b*) and Jackson & McFarlane (1976). Alternatively, they may be triggered exogenously, for example by a build-up of pressure in the enteron (McFarlane, 1974*a*) or by the oxygen concentration of the enteric water falling to a critical level.

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