

## ACTIVITY AND RESPIRATION IN THE ANEMONE, *METRIDIUM SENILE* (L.) EXPOSED TO SALINITY FLUCTUATIONS

SANDRA E. SHUMWAY<sup>1</sup>

*N.E.R.C. Unit of Marine Invertebrate Biology, Marine Science Laboratories, Menai Bridge, Gwynedd, U.K.*

**Abstract:** Activity and respiration in the anemone, *Metridium senile* (L.), were monitored under both constant and fluctuating salinity conditions. During constant exposure to 50% sea water it was found that the animals retracted the tentacles and that the rate of oxygen consumption decreased by  $\approx 50\%$ . The same response was elicited from animals in 100% sea water in a contracted state. Animals exposed to continually fluctuating salinities were found to retract the tentacles, contract the body wall, and produce amounts of mucus during periods of decreasing salinities. These reactions were reversed during exposure to increasing salinity. Oxygen consumption never ceased entirely in animals exposed to dilute sea water and it was found that during declining oxygen tension *M. senile* regulated its oxygen consumption until the environmental oxygen tension fell to  $\approx 30\%$  saturation.

### INTRODUCTION

The existing information on oxygen consumption in sea anemones is often contradictory. Newell & Northcroft (1967) found that *Actinia equina* showed variable rates of oxygen consumption at different experimental temperatures, and interpreted these results in terms of a 'maintenance metabolism' and an 'active metabolism'. Sassaman & Mangum (1970), on the other hand, found no evidence for different levels of oxygen consumption in three species of anemones. A respiratory rhythm has been reported in *Metridium senile* and *Actinia equina* by Jones, Pickthall & Nesbitt, (1977) although Batham & Pantin (1950a, b, c, 1954) in a long study found no evidence for such a rhythm in *Metridium senile*. Respiratory rhythms have, however, been reported for other coelenterates (Brafield & Chapman, 1967; Chapman, 1972).

Although there is some information regarding respiration in anemones, the majority of this information deals with the effects of declining oxygen tension and/or temperature on the respiratory rate. Apart from those of Shoup (1932) there are no studies on the effects of reduced salinities on anemone respiration. Shoup (1932) monitored the rate of oxygen consumption in *M. marginatum* exposed to constantly lowered salinities; however, studies in which animals are transferred directly to reduced salinities have recently been criticized by Stickle & Ahokas (1974), Davenport, Gruffydd & Beaumont (1975), Shumway (1977, in press), and Davenport (1977)

<sup>1</sup> Present address: Portabello Marine Laboratory, Portabello, New Zealand.

since they are uncharacteristic of most environmental situations. The present study was undertaken to determine the effects of gradual salinity changes on both activity and respiration in *M. senile* L.

## MATERIALS AND METHODS

*M. senile* were collected from the Menai Strait, Anglesey and allowed to re-attach in small plastic Petri dishes kept in aquaria supplied with running sea water at 15°C pumped from the Menai Strait (salinity  $\approx 32\text{‰} = 100\text{‰}$  s.w.).

Oxygen consumption was monitored using a larger version of the method described by Davenport (1976). A Radiometer oxygen electrode was connected *via* a Radiometer PHM 71 meter, to a Smiths Servoscribe chart recorder (adjusted to 100 mV). Animals in the size range 0.03–0.8 g freeze-dried weight and experimental chambers in the size range 35 to 400 ml capacity were used and the animals, still attached to a piece of a Petri dish, were placed in their respective chambers for several hours before experiments were started. A magnetic flea was placed in the chamber below the resting platform of the animal and the entire chamber placed in a waterbath over an immersible magnetic stirrer. In some experiments animals were placed in 50‰ sea water and oxygen uptake measured while in others the animals were prodded to induce contraction. The results are expressed as ml O<sub>2</sub> consumed h<sup>-1</sup> animal<sup>-1</sup> ( $V_{O_2}$ ).

The effect of declining oxygen tension on the oxygen uptake of *M. senile* was determined by allowing the animal completely to deplete the O<sub>2</sub> supply. The rate of oxygen consumption during decreasing oxygen tension was plotted against the weight specific oxygen consumption of the animal.

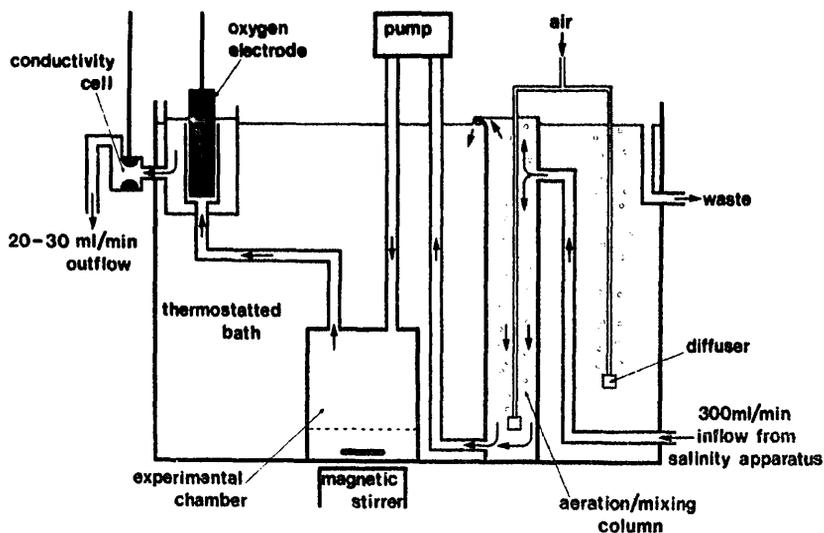


Fig. 1. Apparatus used to monitor oxygen consumption in *M. senile* during exposure to fluctuating salinities.

The apparatus used to produce fluctuating salinity regimes has been described by Davenport *et al.* (1975). Anemones were placed in clear Perspex experimental chambers to facilitate viewing, and were exposed both to gradual (sinusoidal) and abrupt (square-wave) salinity changes (see Fig. 5) fluctuating between 100 and 30‰ sea water. The programmes ran for 24 h. Oxygen consumption by anemones during changing salinities was measured using the system shown in Fig. 1 (Bettison & Davenport, pers. comm.). The animal was placed in the experimental chamber at least 12 h prior to the start of the experiment.

## RESULTS

### OXYGEN CONSUMPTION

Fig. 2 shows the relationship between oxygen uptake at full oxygen tension and the tissue dry weight for *M. senile* determined in 100‰ sea water (Line A), 50‰

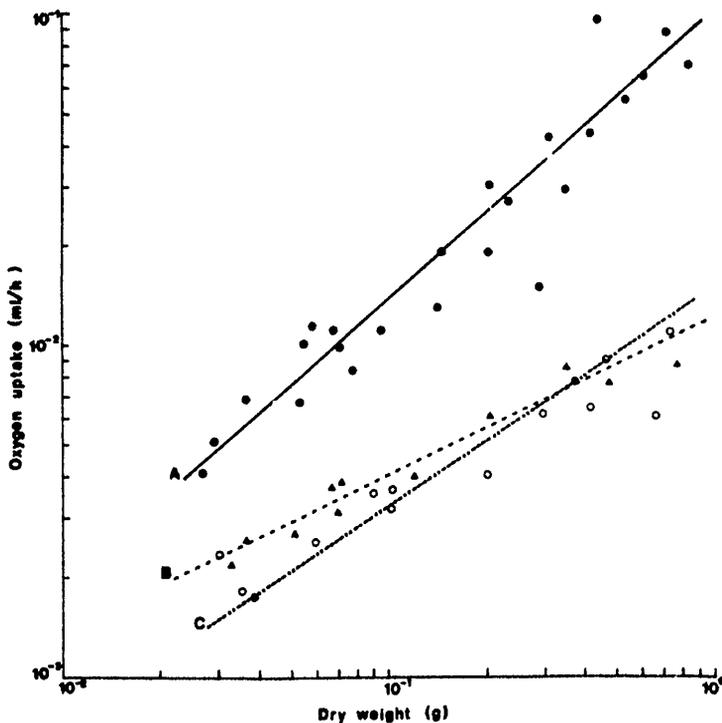


Fig. 2. Oxygen consumption by *M. senile* in 100‰ sea water (Line A; ●), 50‰ sea water (Line B; ▲), and in inactive animal (Line C; ○).

sea water (Line B) and in contracted animals in full strength sea water (Line C). The relationship between oxygen uptake at full oxygen tension, expressed as  $V_{O_2}$ , and tissue dry weight in g may be expressed as: oxygen consumption =  $a$  dry weight <sup>$b$</sup> , where  $a$  is the proportionality factor and  $b$  is a fractional power. The linear regression equations are given in Table I.

There was no significant difference between the slopes of the lines representing inactive animals (Line C) and animals in 50% sea water (Line B); however, both of these lines were found to be significantly different from the line (Line A) representing active animals in 100% sea water.

TABLE I

Linear regression equations of oxygen consumption ( $\log_{10} y$ ) on dry weight ( $\log_{10} x$ : g) for *Metridium senile* (active, inactive and in 50% sea water):  $n$ , number of determinations.

	$n$	$a$	$b$
Active	24	0.1106	0.8901
Inactive	14	0.0149	0.6452
50% sea water	11	0.0128	0.4915

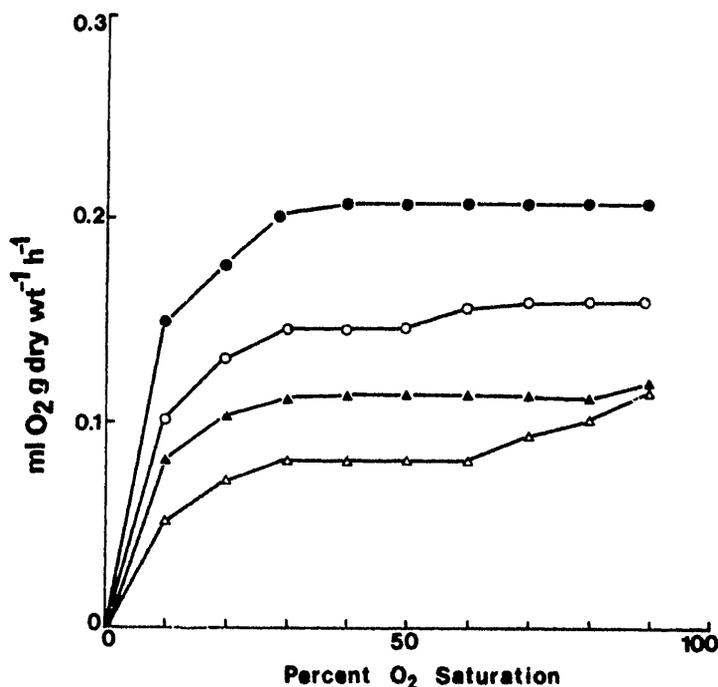


Fig. 3. Oxygen consumption by *M. senile* in declining oxygen tension; the results of four experiments.

Fig. 3 shows the results of four individual experiments in which oxygen consumption was measured relative to oxygen tension. In all the animals studied, the rate of oxygen consumption was independent of the environmental oxygen tension until it fell to  $\approx 30\%$  oxygen saturation ( $\approx 1.7$  ml  $O_2$ /l).

#### ACTIVITY

It was found that when *M. senile* were exposed to gradual salinity changes the animals showed very definite patterns of activity. Fig. 4 shows the relative shapes

and sizes of anemones at various salinities. During exposure to full strength sea water the tentacles were fully exposed and the body was fully extended. As the salinity began to decrease the tentacles were retracted and with further decrease the entire body became contracted. At the lowest sea-water concentration (30‰ sea water) the animal were contracted to  $\approx 1/4$  of their original height. The process was reversed during increasing salinities. The body first became elongated and then when

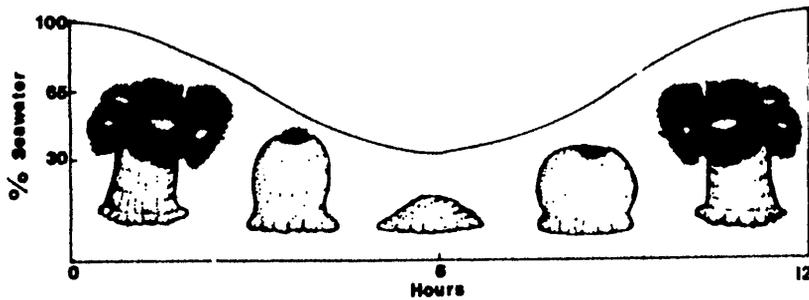


Fig. 4. The effect of fluctuating salinity on activity in *M. senile*: all animals are drawn to the same scale.

the external sea-water concentration had reached full strength (90–100‰) the tentacles reappeared. This pattern was noted in  $\approx 80\%$  of the animals studied; in the other 20% there was no recovery during increasing salinities. All animals were seen to produce copious amounts of mucus during exposure to low salinities and were very active during periods of high salinities, sometimes even 'crawling' about the experimental chamber.

#### OXYGEN CONSUMPTION DURING FLUCTUATING SALINITIES

The oxygen consumption of *M. senile* exposed to gradual and abrupt salinity changes is shown in Fig. 5. Oxygen consumption decreased during decreasing

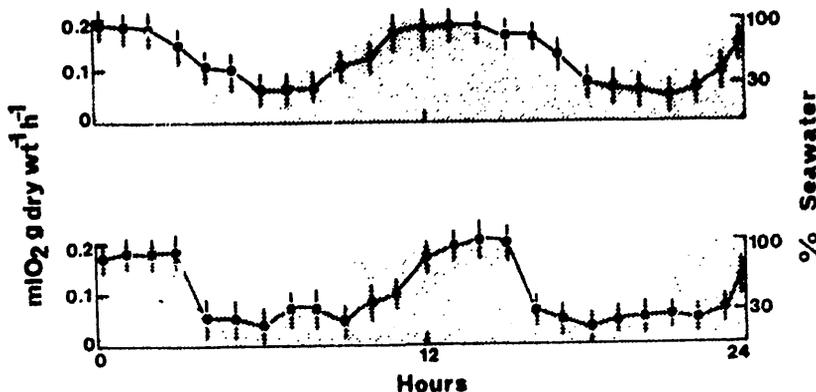


Fig. 5. Oxygen consumption during exposure to (a) 30‰ sea water minimum sinusoidal salinity regime and (b) 30‰ sea water minimum square wave regime: stippled areas represent changes in the external medium: each point mean of 5 animals: error bars represent 95% confidence limits.

salinities but never entirely ceased. During periods of low salinity when the animals were contracted, the rate of oxygen consumption was  $\approx 25\%$  of the original rate. The response is more marked in animals exposed to the abrupt salinity profile and the recovery period is also longer under these conditions.

## DISCUSSION

The retraction of tentacles, contraction of the body wall, and the production of mucus in anemones in response to decreasing salinities is comparable to shell valve closure and/or retraction of the siphons in bivalves, withdrawal into the burrow in lugworms, and closure of the siphons in ascidians exposed to lowered salinities as described previously by Shumway (1977, in press) and Shumway & Davenport (1977). It is evident from this work that *M. senile*, like *M. marginatum* (Shoup, 1932) is readily capable of regulating its distension and surface area in various salinities. Shoup (1932) studied the effects of lowered salinities on oxygen consumption in *M. marginatum* and found that the further away from the optimum concentration of sea water, the greater the decrease. He also noted that a change in the extension of the animals always accompanied any marked change in the rate of oxygen uptake when in an unfavourable medium. The present results confirm these findings. It may be seen from Fig. 5 that the rate of oxygen consumption never entirely ceases when the anemones are exposed to fluctuating salinities, but that it varies in the same way as the salinity profile. There is no evidence of an oxygen debt which confirms the findings of Sassaman & Mangum (1973) that oxygen debt responses are not elicited in *M. senile* unless the animals have completely ceased detectable aerobic metabolism.

Jones *et al.* (1977) have calculated that between  $\approx 50$  and  $90\%$  of the total oxygen requirement of *M. senile* enters the tissues from the ectoderm and Sassaman & Mangum (1972) found that the tentacles account for  $\approx 56\%$  of the total surface area in *M. senile*. When the animals are contracted due to mechanical stimulus or unfavourable external conditions and the tentacles are retracted, the surface area available for the absorption of oxygen is reduced by  $\approx 50\%$ . This is reflected in the low values for *b* obtained from inactive animals and animals exposed to  $50\%$  sea water (Fig. 2, Lines B & C). Fig. 4 shows the changes in body form of the animals and it is clear from Figs 4 and 5 that oxygen consumption is related to the amount of tissue surface area available. When the animals have withdrawn the tentacles, oxygen consumption has decreased by about a half and as the salinity continues to decline and the body becomes contracted to about one quarter of its original size the oxygen consumption also is reduced to  $\approx 25\%$  of its original rate. Oxygen consumption is at its lowest exposure to low salinities when the animals are contracted and at its peak during exposure to full strength sea water. Jones *et al.* (1977) also described a respiratory rhythm in *M. senile* pointing to the gastroderm as the

major site of oxygen consumption. There was no evidence of such a rhythm in anemones in this study, thus supporting the previous work of Sassaman & Mangum (1972) where no periodic irrigation of the coelenteron could be detected and tentacular exchange was concluded to be the predominant site of gaseous exchange with the environment.

Newell & Northcroft (1967) considered that in the anemone *Actinia equina* there were two levels of oxygen consumption in animals which were presumably active and concluded that there were two levels of metabolism in this species. There was no evidence found in this work for more than one type of level of oxygen consumption in active *Metridium senile* at a given experimental temperature (Fig. 2, Line A). Again, the present findings are in agreement with those of Sassaman & Mangum (1970) who support the idea of a continual state of spontaneous, almost rhythmical activity.

The weight specific oxygen consumption rate ( $Q_{O_2}$ ) is given by,  $Q_{O_2} = aW^{b-1}$ . The value of  $b$  for *M. senile* in 100% sea water was found to be 0.890 and so  $b - 1$  is  $-0.110$ . Oxygen consumption increases with increasing size and smaller individuals respire at a faster rate per unit weight than do larger individuals. The values of  $b$  for inactive anemones and animals exposed to 50% sea water were 0.645 ( $b - 1 = -0.355$ ) and 0.491 ( $b - 1 = -0.519$ ), respectively. These values are not significantly different and reflect not just a change in surface availability but a different surface: volume ratio. This in turn implies a gas exchange surface of metabolizing tissue ratio different from that of animals in 100% sea water.

The effect of declining oxygen tensions on the rate of respiration in *M. senile* are shown in Fig. 3. The rate of respiration is almost totally independent of the oxygen concentration of the external medium to  $\approx 30\%$  air saturation. Sassaman & Mangum (1972) found that *M. senile* showed partial or imperfect regulation of the metabolic rate when exposed to declining oxygen tensions and that measurable oxygen consumption ceased at oxygen concentrations above zero. This was not the case in the present study where oxygen consumption continued until all the available oxygen had been utilized.

It is well known that *M. senile* are found intertidally and subtidally in estuaries and in tidepools as well as on pilings *etc.* It is not surprising, therefore, that the anemones have developed a means of adapting to changing salinities as would be experienced in estuaries and declining oxygen tensions as might be experienced in tidepools.

#### ACKNOWLEDGEMENTS

The author would like to thank Mr A. Vardy, University College of North Wales for help with the statistics, Mr M. J. Waldock for the drawing of Fig. 4, Miss J. Bettison and Dr J. Davenport for the use of their unpublished figures and Professor D. J. Crisp, F.R.S. and Dr D. L. Holland for critically reading the

manuscript. This work was carried out under tenure of a fellowship from the Marshall Aid Commemoration Commission.

#### REFERENCES

- BATHAM, E. J. & C. F. A. PANTIN, 1950a. Muscular and hydrostatic action in the sea-anemone *Metridium senile* (L.). *J. exp. Biol.*, Vol. 27, pp. 264-289.
- BATHAM, E. J. & C. F. A. PANTIN, 1950b. Inherent activity in the sea-anemone *Metridium senile* (L.). *J. exp. Biol.*, Vol. 27, pp. 290-301.
- BATHAM, E. J. & C. F. A. PANTIN, 1950c. Phases of activity in the sea-anemone, *Metridium senile* (L.), and their relation to external stimuli. *J. exp. Biol.*, Vol. 27, pp. 377-399.
- BATHAM, E. J. & C. F. A. PANTIN, 1954. Slow contraction and its relation to spontaneous activity in the sea-anemone *Metridium senile* (L.). *J. exp. Biol.*, Vol. 31, pp. 84-103.
- BRAFIELD, A. E. & G. CHAPMAN, 1967. The respiration of *Pteroides griseum* (Bohadsch), a pennatulid coelenterate. *J. exp. Biol.*, Vol. 46, pp. 97-104.
- CHAPMAN, G., 1972. A note on the O<sub>2</sub> consumption of *Renilla köllikeri* Pfeffer. *Comp. Biochem. Physiol.*, Vol. 42A, pp. 863-866.
- DAVENPORT, J., 1976. A technique for the measurement of oxygen consumption in small aquatic organisms. *Lab. Pract.*, Vol. 25, pp. 693-695.
- DAVENPORT, J., LI. D. GRUFFYDD & A. R. BEAUMONT, 1975. An apparatus to supply water of fluctuating salinity and its use in a study of the salinity tolerances of larvae of the scallop *Pecten maximum* L. *J. mar. biol. Ass. U.K.*, pp. 391-409.
- JONES, W. C., V. J. PICKTHALL & S. P. NESBITT, 1977. A respiratory rhythm in sea anemones. *J. exp. Biol.*, Vol. 68, pp. 187-198.
- NEWELL, R. C. & H. R. NORTHCROFT, 1967. A re-interpretation of the effect of temperature on the metabolism of certain marine invertebrates. *J. Zool. Lond.*, Vol. 151, pp. 277-298.
- SASSAMAN, C. & C. P. MANGUM, 1970. Patterns of temperature adaptation in North American coastal actinians. *Mar. Biol.*, Vol. 7, pp. 123-130.
- SASSAMAN, C. & C. P. MANGUM, 1972. Adaptations to environmental oxygen levels in infaunal and epifaunal sea-anemones. *Biol. Bull. mar. Lab., Woods Hole*, Vol. 143, pp. 657-678.
- SASSAMAN, C. & C. P. MANGUM, 1973. Relationship between aerobic and anaerobic metabolism in estuarine anemones. *Comp. Biochem. Physiol.*, Vol. 44A, pp. 1313-1319.
- SHOUP, C. S., 1932. Salinity of the medium and its effect on respiration in the sea anemone. *Ecology*, Vol. 13, pp. 81-85.
- STICKLE, W. B. & R. AHOKAS, 1974. The effects of tidal fluctuation of salinity on the perivisceral fluid composition of several echinoderms. *Comp. Biochem. Physiol.*, Vol. 47A, pp. 469-476.
- SHUMWAY, S. E., 1977. The effect of salinity fluctuation on the osmotic pressure and Na<sup>+</sup>, Ca<sup>2+</sup> and Mg<sup>2+</sup> ion concentrations in the hemolymph of bivalve molluscs. *Mar. Biol.*, Vol. 41, pp. 153-177.
- SHUMWAY, S. E., in press. Respiration, heart rate and pumping activity in *Ciona intestinalis* L. exposed to fluctuating salinities. *Mar. Biol.*
- SHUMWAY, S. E. & J. DAVENPORT, 1977. Some aspects of the physiology of *Arenicola marina* L. exposed to fluctuating salinities. *J. mar. biol. Ass. U.K.*, Vol. 59, pp. 907-927.