

OSMOTIC BALANCE AND RESPIRATION IN THE HERMIT CRAB, *PAGURUS BERNHARDUS*, EXPOSED TO FLUCTUATING SALINITIES

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(Figs. 1-5)

Specimens of *Pagurus bernhardus* (with and without shells) were exposed to both gradual (sinusoidal) and abrupt (square-wave) salinity fluctuations and changes in haemolymph osmolality, tissue water content and oxygen consumption monitored. Oxygen consumption was also monitored under steady-state conditions; under these conditions there was no significant difference between the rate of oxygen consumption by animals with shells and animals without shells. Oxygen consumption was found to vary with body weight according to the equation O_2 consumption = $0.292 W^{0.668}$. During exposure to fluctuating salinities the crabs with shells were seen to increase locomotory activity when the external medium declined to approximately 75% sea water. Haemolymph osmolality values followed the same pattern of change as the external medium; the haemolymph of crabs without shells became significantly more dilute during exposure to low salinity than did that of crabs with shells. *P. bernhardus* showed significant increases and decreases in hydration level as salinities fell and rose respectively. Crabs with shells showed a marked temporary increase in oxygen consumption when the external medium declined to approximately 75% sea water; crabs without shells showed no such response. The importance of the shell as a means of protection against dilute media is discussed.

INTRODUCTION

There is a wealth of information concerning the ionic and osmotic responses of crustaceans to salinity changes; however, the majority of this information deals with animals from the estuarine habitat known to be capable of osmotic and/or ionic regulation. Data for littoral anomuran species are scarce and, as pointed out by Davenport (1972) and Bursey & Bonner (1977), this is probably due to the fact that littoral species might be expected to be stenohaline. Tidepools of the littoral zone are subject to dilution by rain and terrestrial run-off, thus exposing the inhabitant animals to variable salinities.

The hermit crab, *Pagurus bernhardus* (L.), is a common inhabitant of such rocky shore tidepools and of sandy flats and has been shown by Davenport (1972) to exhibit a moderate degree of euryhalinity and a capability for short term volume regulation. The present study was undertaken to study the effects of changing salinity on the respiration and osmotic balance of *P. bernhardus* and to assess the role of the shell as a means of protection against unfavourable environmental conditions.

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MATERIALS AND METHODS

Littoral specimens of *P. bernhardus*, all living in dog-whelk shells, were collected from the intertidal area of the Menai Strait, Anglesey (U.K.), beneath the northern end of the Telford Suspension Bridge. In the laboratory half had their shells removed and half had their shells cleaned of epiphytes. All crabs were then placed in aquaria supplied with running sea water from the Menai Strait for one week prior to use in experiments. The animals were not fed and no attempt was made to separate the sexes; egg-masses attached to females were removed before the crabs were weighed. All experiments were carried out at a temperature of 15 °C; the salinity of 100 % sea water was approximately 32 ‰.

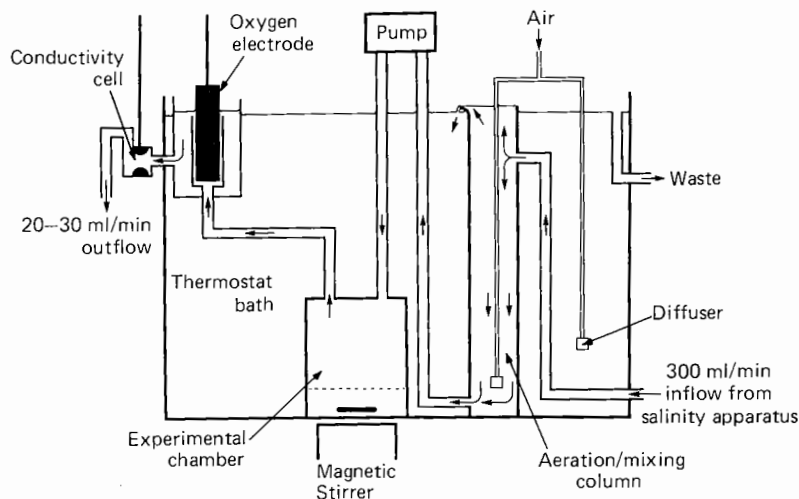


Fig. 1. Apparatus used to monitor oxygen consumption in *P. bernhardus* exposed to fluctuating salinities. (From Bettison & Davenport, in preparation.)

Oxygen consumption by crabs with and without shells was monitored using a scaled-up version of the method described by Davenport (1976). The Radiometer oxygen electrode used was connected via a Radiometer PHM 71 meter, to a Smiths Servoscribe chart recorder (adjusted to 100 mV). Animals in the size range 0.03–1.2 g dry weight were used. The animals were placed in their respective experimental chambers at least 3 h before the start of the experiment. A magnetic flea was placed in the chamber below the resting platform of the animal and the entire chamber placed in a water bath over an immersible magnetic stirrer. Results are expressed as ml O₂ consumed h⁻¹ animal⁻¹ (V_{O_2}).

Davenport, Gruffydd & Beaumont (1975) described the apparatus used to produce fluctuating salinity regimes. Crabs were placed in the experimental chamber 24 h prior to experimentation and were exposed both to gradual (sinusoidal) and abrupt (square wave) salinity changes (see Figs. 3–5) fluctuating between 100 ‰ and 50 ‰ sea water. Minimum sea-water concentrations lower than 50 ‰ were found to be lethal. The programmes ran for 24 h. Five animals were removed from the experimental chamber each hour, weighed (without shells) and a haemolymph sample collected by piercing the pericardial cavity with a finely drawn out glass capillary. Haemolymph osmolality was measured using a Halbmikro Osmometer. The animals were then frozen, freeze dried and reweighed to determine total body water.

Oxygen consumption during changing salinities in the hermit crabs was measured using the system shown in Fig. 1 (Bettison & Davenport, in preparation). Control air-saturated oxygen levels were established at will by moving the electrode from the position shown in Fig. 1 to the thermostat bath (aerated by compressed air). Five animals were placed in the experimental chamber

at least 24 h prior to the start of the experiment and the results are expressed as ml O₂ consumed h⁻¹ g dry wt⁻¹. Six experiments were carried out using animals with shells and repeated for animals without shells.

RESULTS

Oxygen consumption

Fig. 2 shows the relationship between oxygen uptake at full oxygen tension and the tissue dry weight for *P. bernhardus* determined in animals with shells and in animals

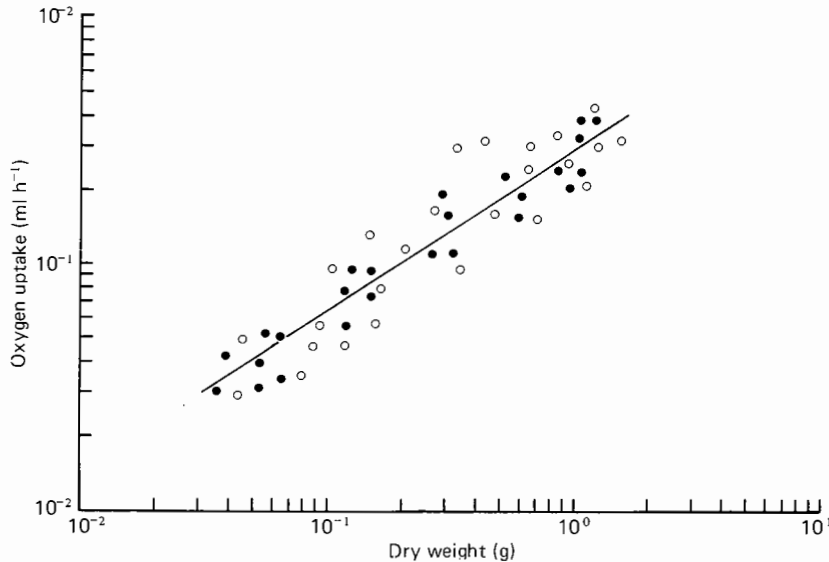


Fig. 2. Oxygen consumption by *P. bernhardus* with shells (●) and without shells (○).

Table 1. Linear regression equations of oxygen consumption ($\log_{10} Y$) on dry weight ($\log_{10} X$:g) for *P. bernhardus* with and without shells

The number of determinations (n) and the correlation coefficient (r) ($P < 0.001$ for both lines) are also given.

	n	a	b	$b-1$	r
With shells	25	0.292	0.668	0.332	0.966
Without shells	25	0.299	0.676	0.324	0.902

without shells. The relationship between oxygen uptake at full oxygen tension, expressed as V_{O_2} and tissue dry weight in g may be expressed as:

$$V_{O_2} = a \text{ dry weight}^b,$$

where a is the proportionality factor and b is a fractional power. The linear regression equations and correlation coefficients for the data shown in Fig. 2 are given in Table 1. Only one line is drawn in Fig. 2 as it is impossible to distinguish one set of data from the other.

*Responses of P. bernhardus to fluctuating salinities**Activity*

During periods of decreasing salinity, crabs with shells were seen to become very active, actually running about the experimental chamber when the external salinity reached approximately 75% sea water, after which the animals became quiescent in the shells until the salinity rose. Crabs without shells showed little or no activity during any period of the salinity profile.

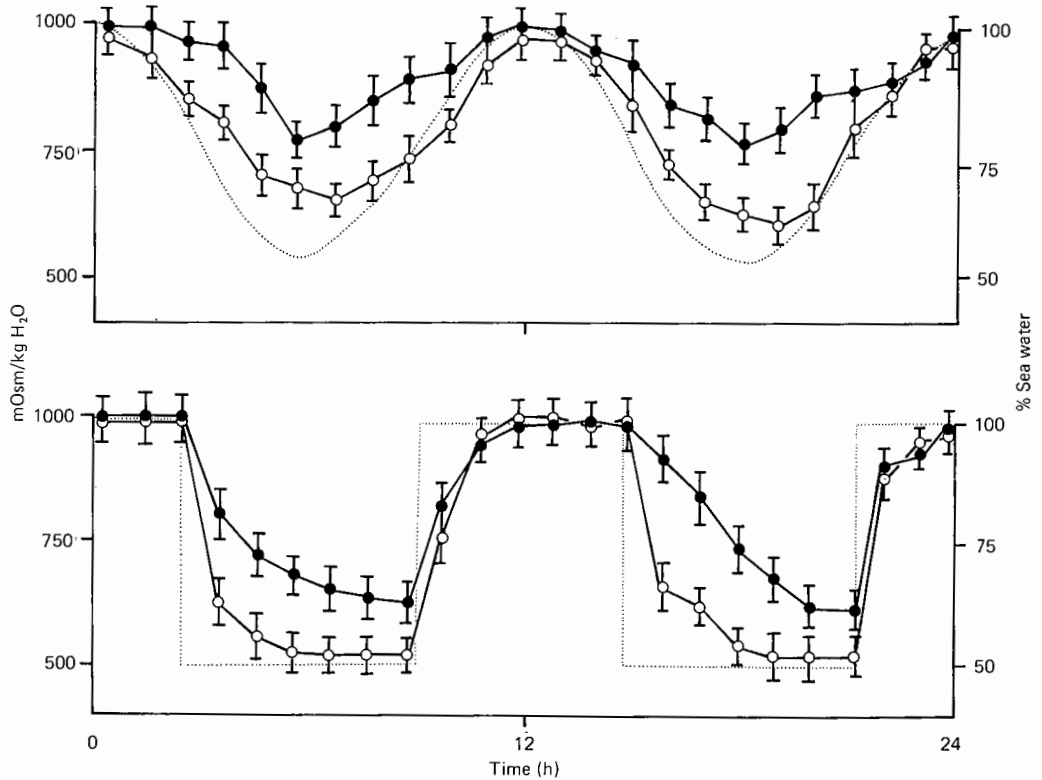


Fig. 3. Changes in haemolymph osmolality of *P. bernhardus* exposed to fluctuating salinities; (●) with shells, (○) without shells. Error bars represent 95% confidence limits.

Osmotic changes

Fig. 3 shows the changes in haemolymph osmolality of *P. bernhardus* during exposure to a 50% sea-water minimum sinusoidal fluctuation. The haemolymph osmolality values followed the same pattern of change as the external medium and there was evidence of a time lag between haemolymph and sea-water concentration. The haemolymph of crabs without shells became significantly more diluted during exposure to low salinity than did the haemolymph of crabs with shells.

Tissue water

When placed both in the sinusoidal and abrupt regimes (Fig. 4) *P. bernhardus* showed significant increases and decreases in hydration level as salinities fell and rose respectively. Animals without shells showed significantly greater changes in tissue water content than did animals with shells.

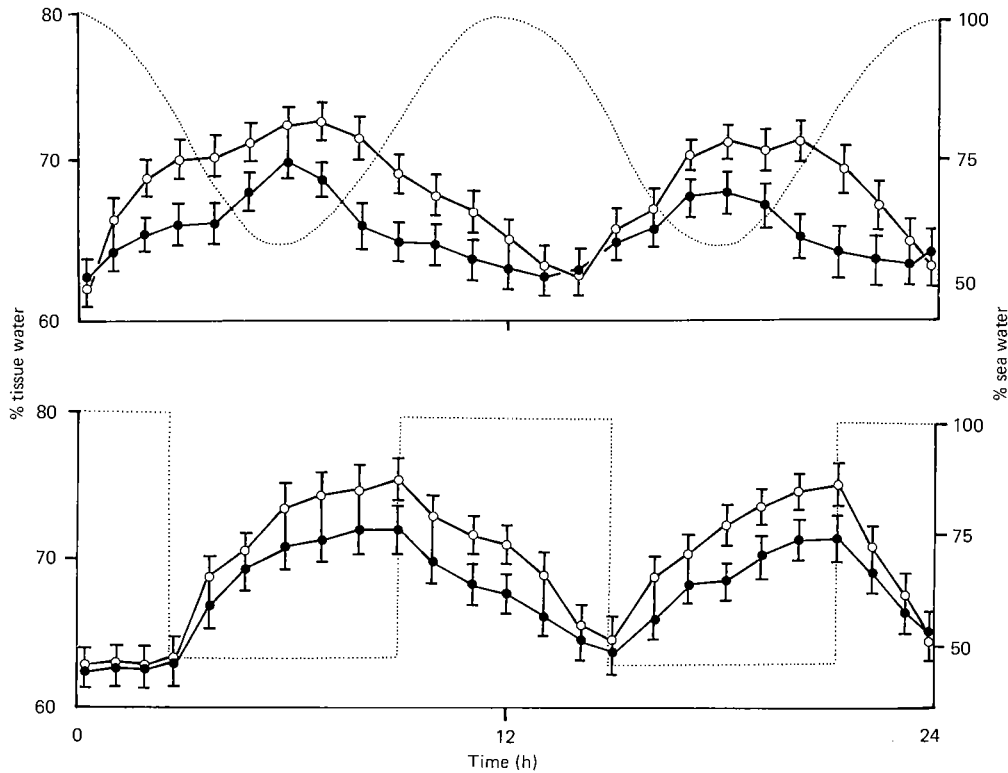


Fig. 4. Changes in total tissue water of *P. bernhardus* exposed to fluctuating salinities; (●) with shells, (○) without shells. Error bars represent 95% confidence limits.

Oxygen consumption

The oxygen consumption of specimens of *P. bernhardus* exposed to gradual and abrupt salinity changes is shown in Fig. 5. Crabs with shells showed a marked temporary increase in oxygen consumption when the external medium declined to approximately 75% sea-water and then returned to the original level. The response was repeated during the second cycle of the salinity profile. Crabs without shells, on the other hand, showed no change in oxygen consumption rate throughout the salinity profile.

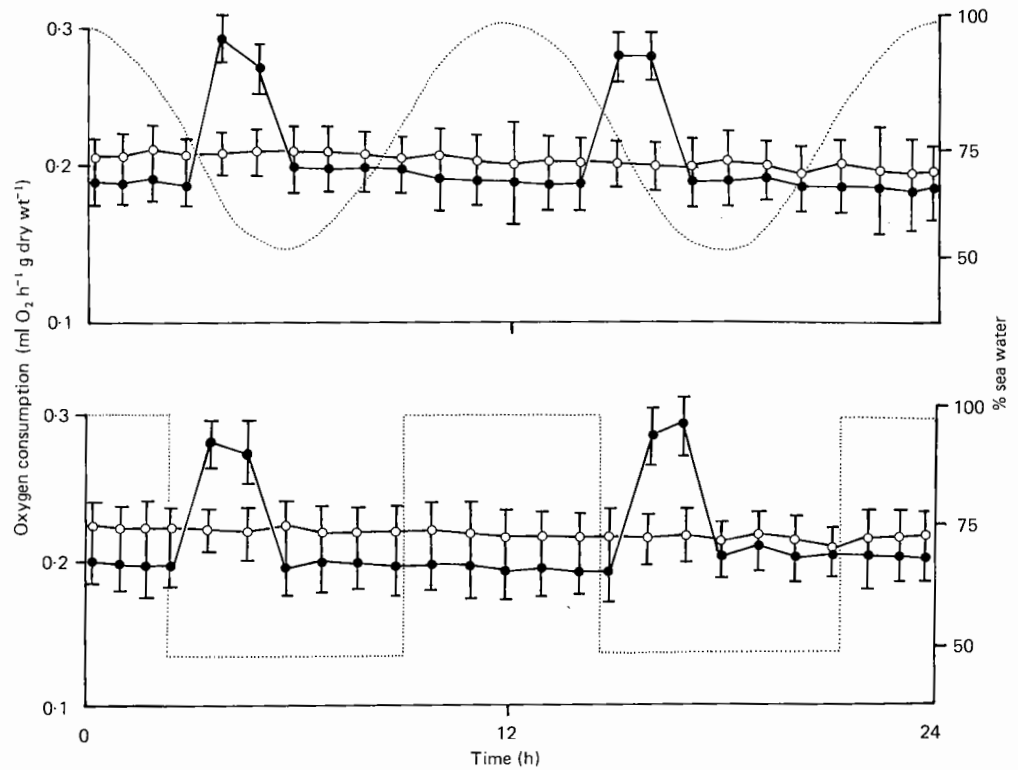


Fig. 5. Changes in oxygen consumption of *P. bernhardus* during exposure to fluctuating salinities. (●) with shells, (○) without shells. Error bars represent 95% confidence limits.

DISCUSSION

The rate of oxygen consumption (V_{O_2}) is proportional to a fractional power (b) of the body weight (W) such that:

$$V_{O_2} = aW^b,$$

where a is the proportionality factor.

The weight specific oxygen consumption rate (Q_{O_2}) is then given by:

$$Q_{O_2} = aW^{b-1}.$$

The b value for *P. bernhardus* in this study was found to be 0.668 and $b-1$ is therefore -0.332. As expected, this indicates that oxygen consumption increases with increasing size in *P. bernhardus* but that smaller individuals respire at a faster rate per unit weight and unit time than do larger animals. This b value is in close agreement with the b value of 0.664 reported by Roberts (1957) for *Pachygrapsus crassipes*, but differs from that reported for *Pugettia producta* ($b = 0.8$) by Weymouth *et al.* (1944). There was no significant difference between the b values calculated for hermit crabs with and without shells.

The importance of the shell as a means of protection against osmotic changes and swelling is clearly shown in Figs. 3 and 4. Although animals with shells showed significant

changes in haemolymph osmolality and total tissue water content during changing salinities, animals without shells showed far greater changes and were seen to become extremely swollen, thus impairing mobility in some cases. This protection is seen most readily in the animals exposed to the abrupt salinity regime where the blood osmolality of crabs with shells fell to approximately 650 m-osmole after 6 h in 50% sea water, while that of crabs without shells was virtually isosmotic (500 m-osmole) with the external medium after only 2–3 h. Davenport (1972) found that *P. bernhardus* placed in 60% sea water swelled by 15.4% during the first hour, slightly but not significantly more in the second hour and then lost weight. In the present experiment, animals exposed to a 50% sea-water abrupt salinity programme ('steady state' for 6 h) showed an increase in tissue water content during the first 3 h of exposure but no decrease in tissue water was noted until the animals were returned to full strength sea water. There are two possible explanations for this discrepancy. One is that handling of the animals during weighing and returning them to the dilute sea water caused the observed decrease in tissue water, but this seems unlikely. The second is that since 50% sea water is the minimum that this species was found to tolerate it is possible that the mechanism for volume regulation described by Davenport (1972) for animals in 60% sea water is destroyed or impaired and takes longer to become effective in animals exposed to this lower sea-water concentration.

As seen in Fig. 5 there is a marked temporary increase in oxygen consumption by crabs with shells when exposed to dilute sea water. It has been proposed by McFarland & Pickens (1965) that the increase in oxygen consumption rate at lowered salinities is due to a combination of increased osmoregulatory work and an increase in locomotory activity. Dehnel (1960), on the other hand, has suggested that the increased oxygen consumption measurements found at low salinities is the result of increased osmotic and not the result of increased muscular activity. Both of these authors were dealing with animals capable of osmoregulation and it is therefore likely that the increase in oxygen consumption noted in their studies is due for the most part to increased osmoregulatory work. The crabs used in this study, however, are known to be osmotic conformers. It is possible that the increased oxygen consumption noted in animals exposed to decreased salinity is due in part to the volume regulation process described by Davenport (1972), but since the animals without shells showed so much increase and Davenport based his theory on animals without shells, this seems unlikely. More likely, since only animals with shells were seen to increase their activity in the experimental chambers during low salinity it is most probable that the noted temporary increase in oxygen consumption during exposure to these low salinities is due to this increased activity. Extremely low salinity is an adverse condition to which the animals may well react by escape, and escape reactions are reflected as changes in locomotory activity. Although these animals have been shown to be capable of some volume regulation (Davenport, 1972) and have been shown in this study to be tolerant of fluctuating salinities, their first reaction to low salinity is to escape and failing this to withdraw into their shells. This withdrawal into the shell during adverse salinity conditions is akin to the mechanism of shell valve closure in bivalves, withdrawal of the tentacles, contraction of the body wall and mucus production in *Metridium*, closure of the siphons in *Ciona*, quiescence in the burrow of

Arenicola and opercular flap closure in barnacles previously described by Shumway (1977; in preparation), Shumway & Davenport (1977) and Davenport (1976). It is proposed that when escape is impossible, hermit crabs withdraw into their shells and await more favourable conditions.

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REFERENCES

- BURSEY, C. R. & BONNER, E. E., 1977. Osmotic regulation and salinity tolerance of the mole crab, *Emerita talpoida* (Say). *Comparative Biochemistry and Physiology*, **57A**, 207-210.
- DAVENPORT, J., 1972. Volume changes shown by some littoral anomuran crustacea. *Journal of the Marine Biological Association of the United Kingdom*, **52**, 863-877.
- DAVENPORT, J., 1975. A technique for the measurement of oxygen consumption in small aquatic organisms. *Laboratory Practice*, **10**, 693-695.
- DAVENPORT, J., 1976. A comparative study of the behaviour of some balanomorph barnacles exposed to fluctuating sea water concentrations. *Journal of the Marine Biological Association of the United Kingdom*, **56**, 889-907.
- DAVENPORT, J., GRUFFYDD, LL.D D. & BEAUMONT, A. R., 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 maximus* L. *Journal of the Marine Biological Association of the United Kingdom*, **55**, 391-409.
- DEHNEL, P. A., 1962. Aspects of osmoregulation in two species of intertidal crabs. *Biological Bulletin. Marine Biological Laboratory, Woods Hole, Mass.*, **122**, 208-227.
- McFARLAND, W. N. & PICKENS, P. E., 1965. The effects of season, temperature and salinity on standard and active oxygen consumption of the grass shrimp *Palaemonetes pugio* Say. *Canadian Journal of Zoology*, **43**, 571-585.
- ROBERTS, J. L., 1957. Thermal acclimation of metabolism in the crab *Pachygrapsus crassipes* Randall. II. The influence of body size, starvation and molting. *Physiological Zoölogy*, **30**, 232-242.
- SHUMWAY, S. E., 1977. Effect of salinity fluctuation on the osmotic pressure and Na⁺, Ca²⁺ and Mg²⁺ ion concentrations in the hemolymph of bivalve molluscs. *Marine Biology*, **41**, 153-177.
- SHUMWAY, S. E. & DAVENPORT, J., 1977. Some aspects of the physiology of *Arenicola marina* (Polychaeta) exposed to fluctuating salinities. *Journal of the Marine Biological Association of the United Kingdom*, **57**, 907-924.
- WEYMOUTH, F. W., CRISMON, J. M., HALL, V. E., BELDING, H. S. & FIELD, J., 1944. Total and tissue respiration in relation to body weight: a comparison of the kelp crab with other crustaceans and with mammals. *Physiological Zoölogy*, **17**, 50-71.

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- BURSEY, C. R. & BONNER, E. E., 1977. Osmotic regulation and salinity tolerance of the mole crab, *Emerita talpoida* (Say). *Comparative Biochemistry and Physiology*, **57A**, 207-210.
- DAVENPORT, J., 1972. Volume changes shown by some littoral anomuran crustacea. *Journal of the Marine Biological Association of the United Kingdom*, **52**, 863-877.
- DAVENPORT, J., 1975. A technique for the measurement of oxygen consumption in small aquatic organisms. *Laboratory Practice*, **10**, 693-695.
- DAVENPORT, J., 1976. A comparative study of the behaviour of some balanomorph barnacles exposed to fluctuating sea water concentrations. *Journal of the Marine Biological Association of the United Kingdom*, **56**, 889-907.
- DAVENPORT, J., GRUFFYDD, LL.D D. & BEAUMONT, A. R., 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 maximus* L. *Journal of the Marine Biological Association of the United Kingdom*, **55**, 391-409.
- DEHNEL, P. A., 1962. Aspects of osmoregulation in two species of intertidal crabs. *Biological Bulletin. Marine Biological Laboratory, Woods Hole, Mass.*, **122**, 208-227.
- McFARLAND, W. N. & PICKENS, P. E., 1965. The effects of season, temperature and salinity on standard and active oxygen consumption of the grass shrimp *Palaemonetes pugio* Say. *Canadian Journal of Zoology*, **43**, 571-585.
- ROBERTS, J. L., 1957. Thermal acclimation of metabolism in the crab *Pachygrapsus crassipes* Randall. II. The influence of body size, starvation and molting. *Physiological Zoölogy*, **30**, 232-242.
- SHUMWAY, S. E., 1977. Effect of salinity fluctuation on the osmotic pressure and Na⁺, Ca²⁺ and Mg²⁺ ion concentrations in the hemolymph of bivalve molluscs. *Marine Biology*, **41**, 153-177.
- SHUMWAY, S. E. & DAVENPORT, J., 1977. Some aspects of the physiology of *Arenicola marina* (Polychaeta) exposed to fluctuating salinities. *Journal of the Marine Biological Association of the United Kingdom*, **57**, 907-924.
- WEYMOUTH, F. W., CRISMON, J. M., HALL, V. E., BELDING, H. S. & FIELD, J., 1944. Total and tissue respiration in relation to body weight: a comparison of the kelp crab with other crustaceans and with mammals. *Physiological Zoölogy*, **17**, 50-71.