Physiological studies on *Marphysa gravelyi*
VII. Tissue respiration[1]

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KURZFASSUNG: Physiologische Untersuchungen an *Marphysa gravelyi*. VII. Gewebsatmung. Die respiratorische Aktivität des Körpergewebes von *Marphysa gravelyi* SOUTHERN, einem brackwasserlebenden Polychaeten, wurde in verschiedenen Salinitätsstufen (10, 14, 17 und 24 ‰ S) gemessen. Es wurde festgestellt, daß mit zunehmendem Salzgehalt des Mediums der Sauerstoffverbrauch steigt. Diese Zunahme der Atmungsgröße wird in Beziehung zu einer verstärkten Ionenregulation gesetzt. Auf Grund osmoregulatorischer Befunde wird angenommen, daß bei dieser Art Tendenzen zur Anpassung an eine Existenz im Süßwasser bestehen.

INTRODUCTION

The energy required for osmotic regulation has often been a subject of study by determining the oxygen uptake (see POTTS & PARRY 1964). The studies available on polychaetes were carried out mostly on adult whole worms (TARUSSOV 1927, SCHLIEPER 1929a, b, BEADLE 1931, BOSWORTH et al. 1936, TOPPING & FULLER 1942) and as "it is obvious that much of the extra respiration recorded in these experiments on whole animals is not connected with osmotic or ionic regulation at the body surface" (BEADLE 1957), a study of the respiration of body tissues needs no emphasis. Since *Marphysa gravelyi* SOUTHERN exhibited a certain degree of ionic regulation under heterosmotic stress, (KRISHNAMOORTHI 1963, KRISHNAMOORTHI & KRISHNASWAMY 1965, 1966e) implying ion transport, the present study was undertaken in order to explore the energy requirements of body tissues to meet this demand.

MATERIAL AND METHODS

The rate of oxygen consumption was determined with the help of the Warburg constant-volume respirometer (Gallenkamp) (see DIXON 1952 for description) by the

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direct method (with 0.3 cc of 20 %/o KOH in the well) and at a constant rate of 60 oscillations per minute. Thin slices of body tissues, ranging in dry weight from 1 mg to 6.8 mg, were used. Experimental media (5 cc) of desired strengths were made from filtered (No. 40 Whatman starch-free filter paper) sea-water of 34 %/oo salinity as "sea-water is a satisfactory medium for the isolated tissues of most marine worms" (Lockwood 1961, p. 216). All experiments were performed in a cold room at a temperature of 16° C; the temperature of the bath was maintained at 28.0° ± 0.5° C, since all earlier experiments (Krishnamoorthi & Krishnaswamy 1966a, b, c, d, e) were made at this temperature. A period of 15 minutes was allowed for equilibration previous to recording the changes on the manometers. Readings were taken every 15 minutes; no experiment lasted for more than an hour and a half.

RESULTS

The mean rates of oxygen consumption (μl/mg/hr) of tissues exposed to the four different experimental salinities 10 %/oo, 14 %/oo, 17 %/oo and 24 %/oo, are set out in Table 1; they are diagrammatically represented as histograms in Figure 1. The lowest rate of 3.13 μl/mg/hr was obtained in the lowest salinity of 10 %/oo, and the maximum rate of 6.34 μl/mg/hr in the highest salinity of 24 %/oo. In the other two salinities of 14 %/oo and 17 %/oo, the rates of oxygen consumption were respectively 4.07 and 5.28 μl/mg/hr. In other words, the rate of oxygen consumption increased with increasing concentration of the experimental medium as indicated by the 't' values for the significance of the difference between two sample means in Table 1. It may, therefore, be concluded that the rate of oxygen consumption is, perhaps, a function of the osmotic stress – in the present case the salinity – imposed. Similar trends have been reported for Nereis diversicolor and Perinereis cultrifera by CO_2 measurements (Tarussov 1927) and by O_2 uptake (Schlieper 1929a, b, Beadle 1931) for whole adult worms.

The data from Table 1 may be incorporated in the formula:

$$O_2 = aW^b$$
$$\text{or } \log O_2 = \log a + b \log W$$

where O_2 is the rate of respiration or oxygen consumption, W is weight of tissue per whole animal, and a and b two constants; the four resulting formulae are:

(1) 10 %/oo S: $O_2 = 4.125 \, W^{-0.3961}$ or
                   $\log O_2 = \log 4.125 + (- 0.3961 \log W)$
(2) 14 %/oo S: $O_2 = 6.434 \, W^{-0.8167}$ or
                   $\log O_2 = \log 6.434 + (- 0.8167 \log W)$
(3) 17 %/oo S: $O_2 = 5.622 \, W^{-0.1863}$ or
                   $\log O_2 = \log 5.622 + (- 0.1863 \log W)$
(4) 24 %/oo S: $O_2 = 7.330 \, W^{-0.9945}$ or
                   $\log O_2 = \log 7.330 + (- 0.9945 \log W)$

It is thus seen, that, except in 17 %/oo, the 'b' values increase with increasing concentration and this trend supports the previous assumption that O_2 consumption may be a function of the osmotic stress imposed.

Table 1

Rate of oxygen consumption (µl/mg/hr) of body tissues of *M. gravelyi* SOUTHERN, a eunicid brackish-water polychaete, under heterosmotic stress. Temperature of the bath: $28.0° ± 0.5°$ C

Experiment No.	10‰ S			14‰ S			17‰ S			24‰ S		
	Dry weight of tissue (mg)	Total oxygen consumption (µl/hr)	Rate of oxygen consumption (µl/mg/hr)	Dry weight of tissue (mg)	Total oxygen consumption (µl/hr)	Rate of oxygen consumption (µl/mg/hr)	Dry weight of tissue (mg)	Total oxygen consumption (µl/hr)	Rate of oxygen consumption (µl/mg/hr)	Dry weight of tissue (mg)	Total oxygen consumption (µl/hr)	Rate of oxygen consumption (µl/mg/hr)
1	4.6	17.72	3.85	4.0	19.02	4.75	2.5	14.29	5.72	2.0	4.14	2.07
2	4.3	17.90	4.16	3.5	8.36	2.39	2.5	14.90	5.96	3.0	25.57	8.52
3	6.8	17.51	2.43	3.0	10.65	3.55	2.5	9.32	3.73	2.0	3.20	1.60
4	5.1	8.30	1.63	2.5	4.61	1.84	3.0	7.15	3.38	2.5	6.97	2.79
5	3.4	7.19	2.12	3.5	6.39	1.83	2.0	7.99	3.99	2.0	2.66	1.33
6	3.5	7.64	2.18	4.5	5.57	1.24	1.0	4.18	4.18	1.5	3.07	2.05
7	4.5	7.59	1.69	2.5	3.07	1.23	1.5	12.38	8.26	1.5	6.39	4.26
8	3.5	16.91	4.83	2.0	7.99	3.99	2.5	12.30	4.92	1.0	4.18	4.18
9	3.0	15.98	5.33	2.3	5.57	2.42	1.7	12.79	7.52	1.0	3.99	3.99
10	3.0	9.76	3.25	2.6	6.66	2.56	1.5	11.15	7.43	1.5	7.68	5.12
11	3.0	10.65	3.55	2.0	6.15	3.07	2.0	10.65	5.33	1.5	15.98	10.65
12	3.0	3.17	1.06	2.1	5.79	2.76	1.0	4.61	4.61	1.0	9.76	9.76
13	2.5	3.20	1.28	2.7	11.15	4.13	1.0	7.39	7.39	1.0	11.98	11.98
14	2.5	1.39	0.56	2.3	11.98	5.21	1.5	4.18	2.79	1.0	6.15	6.15
15	3.5	1.33	0.38	2.0	9.22	4.61	1.5	5.33	5.33	1.5	6.39	6.39
16	2.0	18.61	9.31	1.5	12.79	8.52	2.0	7.68	5.12	1.0	13.94	9.29
17	1.5	10.75	7.17	2.0	11.15	5.57	2.0	9.59	4.79	1.0	11.98	11.98
18	1.5	3.20	2.13	1.0	9.32	9.32	1.0	6.97	3.48	1.8	7.68	4.27
19	2.0	6.97	3.48	1.0	7.68	7.68	1.5	5.33	5.33	1.5	14.38	9.59
20	2.5	5.33	2.13	1.5	4.79	3.20	1.5	6.15	4.10	1.5	9.76	6.50
21				1.0	5.57	5.57	2.0	9.59	6.39	1.0	10.65	10.65
22				1.0	3.99	3.99	2.0	12.54	6.27			
23							1.5	9.32	6.21			
Mean values			3.13			4.07			5.28			6.34
Standard deviation			1.51			2.26			1.54			3.56
Standard error			0.356			0.481			0.321			0.777
				Between 10‰ and 14‰			Between 10‰ and 17‰			Between 10‰ and 24‰		
't' value				1.571			4.857			3.756		
d.f.				40			41			39		
p				10% < 20%			1%			1%		

DISCUSSION AND CONCLUSIONS

Literature reports on respiratory studies among polychaetes are available only with respect to *Nereis diversicolor, Perinereis cultrifera* and *N. virens* (TARUSSOV 1927, SCHLIEPER 1929a, b, BEADLE 1931, BOSWORTH et al. 1936, TOPPING & FULLER 1942). But these experimentors used whole worms subjected to the stresses of varying anisotonic external concentrations. Since I studied the respiration of body tissues, a comparison is rather difficult. Furthermore, the methods of determination of oxygen uptake differ from each other. Nevertheless, a consideration of trends of oxygen uptake as obtained in the present study and on *N. diversicolor* by BEADLE (1931), reveals a rather unexpected feature. In both cases the increase in oxygen uptake with increasing salinity needs to be explained.

The idea that increased metabolism, as reflected by increased respiratory rates, is due to increased osmotic work has been put forward on many occasions both with reference to polychaetes (SCHLIEPER 1929a, b, BEADLE 1931) and crustaceans (MARGARIA 1931, SCHWABE 1933, FLEMISTER & FLEMISTER 1951). But more recently this has been questioned, e. g., by PIEH (1936) and KROGH (1939). LOFTS (1956) suspected that salinity changes "not only affect the osmoregulatory mechanism but also some other process which causes a large increase in total metabolic rate" in *Palaemonetes varians;* and GROSS (1957) argued that increased rates of respiration "cannot be interpreted as the manifestation of that increased work, for other activities, stimulated by
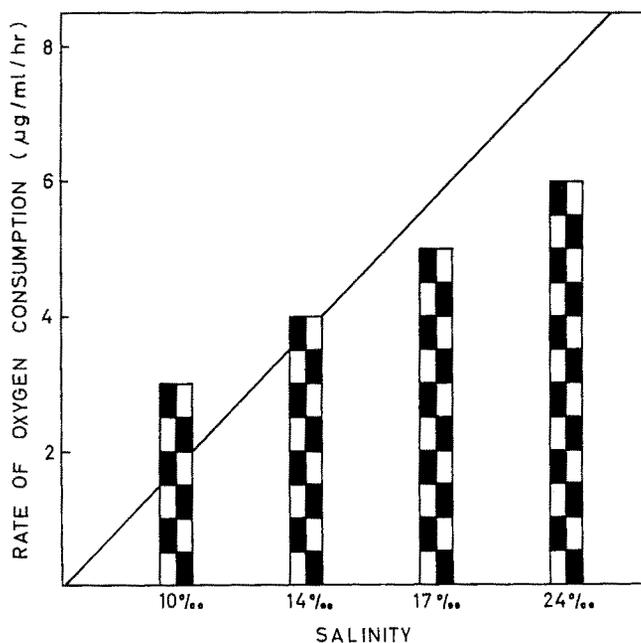

Fig. 1: Rate of oxygen consumption (μl/mg/hr) of body tissues of *M. gravelyi* under heterosmotic stresses. Temperature: 28.0^0 ± 0.5^0 C. Diagonal: line of isosmocity

the stress, e. g., struggle to escape, cannot be isolated". That the extra energy required for osmoregulation in any way, is too small to account for the respiratory differences, has also been stressed by POTTS (1954) and POTTS & PARRY (1964).

In the light of the above views it is difficult to explain the similarity of trends observed between the oxygen uptake of tissues of the body of *M. gravelyi*, as reported here, and those reported for whole *N. diversicolor* by SCHLIEPER (1929a, b) and BEADLE (1931) unless the energetics of osmoregulation are known. However, CROGHAN (1961) points out that if ion transport is "via an energy-rich bond, the energy required will depend upon the rate at which solute is transported and not upon the relative concentrations of the internal and external media" (quoted from ELTRINGHAM 1965). ZERAHN (1956) and KIRSCHNER (1961) have arrived at the same conclusions as CROGHAN. This implies that any change in respiratory rates should be traced to, and be explained in terms of, the efficiency of an ion transport system at work, rather than to the work of osmoregulatory mechanisms involved.

In *M. gravelyi* it has already been shown that not only chlorides, sodium and potassium may be regulated but also the total free amino acids (KRISHNAMOORTHI & KRISHNASWAMY 1966d) and the total carbohydrates (KRISHNAMOORTHI 1966). These facts imply that *M. gravelyi* resorts to transport and mobilization of both inorganic and organic ions for maintaining a constant internal milieu which may require an increased oxygen uptake with increasing salinity to meet the considerable demands of the ion transport system in operation. Such assumption is in agreement with the view expressed by CROGHAN (1961).

Other evidence in support of the above conclusion, could perhaps be the respiratory rates considered in relation to the line of isosmocity. If the line of isosmocity is drawn (Fig. 1), it is seen that in 10 $^0/_{00}$ and 14 $^0/_{00}$, the rates of oxygen uptake exceed the line of isosmocity whereas in the rest of the media they do not. Earlier experiments on *M. gravelyi*, have shown that its body fluid concentration was perhaps isosmotic with a medium of about 40 to 45 $^0/_0$ sea-water corresponding to salinities of 14 $^0/_{00}$ to 15 $^0/_{00}$ (KRISHNAMOORTHI & KRISHNASWAMY 1966c). One may assume, therefore, that 10 $^0/_{00}$ and 14 $^0/_{00}$ represent hyposmotic, and 17 $^0/_{00}$ and 24 $^0/_{00}$ hyperosmotic, media. It is common knowledge that in a hypo-regulator adjustment to hyposmotic media generally involves considerable ion exchange, whereas in a hyper-osmotic medium conservation of both water and salts is a necessity and, therefore, comparatively little ion transport is involved. The increase in respiratory rate in the two hyposmotic media supports the conclusion that it represents a consequence of ion transport, rather than of the relative differences between internal and external concentrations as suggested by CROGHAN (1961).

The value of the regression coefficient 'b' has been the subject of many studies in recent years and values from 1.0 to negative numbers have been reported for whole organisms (BRODY 1945, ZEUTHEN 1953). Similar studies on the 'b' values of excised tissues are sparingly documented. WEYMOUTH et al. (1944) reported the usual negative weight-specific regression in the respiratory rate of the mid-gut gland of *Pugettia producta* but found QO_2 to be higher weight-specifically compared with whole animals. VERNBERG (1956) observed that gill tissue, compared with mid-gut tissue,

respires in nine species of crabs, at a faster rate and was habitat related. In both *Hemigrapsus nudus* and *H. oregonensis*, DEHNEL & McCAUGHRAN (1964) found the 'b' values to vary between − 0.333 and − 0.685 in whole animals, but to be remarkably constant (− 0.169) in gill tissues under all experimental conditions. In *M. gravelyi*, the 'b' values of the respiratory rate of the body tissue, however, vary from − 0.1863 to − 0.9945 in the four experimental salinites tested. How these values would compare with 'b' values of whole animals is not known. The wide range of 'b' values obtained in the present study appears to be related to the various metabolic types proposed by VON BERTALANFFY (1951) and VON BERTALANFFY & KRYWIENCZYK (1953). This is rather unusual especially when the experimental material involved represents the same kind of body tissue. It seems, therefore, reasonable to conclude that not too much significance need be attached to 'b' values; 'b' seems to assume a value which in all probability "is dependent upon inherent properties of the tissue, the total environmental history of the animal, and perhaps even the methods employed in measuring the oxygen consumption" (DEHNEL & McCAUGHRAN 1964, p. 256).

It may not be inappropriate here to examine features of adaptation for clues that are likely to shed some light on the trend of evolution of *M. gravelyi*. In this regard, (1) reduction in permeability and (2) lowering of the body fluid concentration, appear to be of some importance. BEADLE & CRAGG (1940a, b) and BEADLE (1943) are of the opinion that adaptation to freshwater has evolved via two stages, namely, (a) development of mechanisms for absorption of ions and (b) lowering of blood concentration. Examining this concept more closely, CROGHAN (1961) argues that adaptation to a dilute medium involves not only (a), but also adaptations such as decreased permeability of the external surface, and/or (b). It is not known whether *M. gravelyi* possesses a mechanism for absorption of ions. But unlike other polychaetes, *M. gravelyi* is a hyporegulator (KRISHNAMOORTHI & KRISHNASWAMY 1966c) and the well developed branchiae along the entire length of the worm (AIYAR 1933) may well be the site of absorption or excretion of ions, as are the gills in crustaceans and teleosteans (the majority of these hyporegulates and extra-renal regulation is not uncommon; LOCKWOOD 1962). That the uptake of organic material like glycine is possible among brackish water annelids has recently been demonstrated (STEPHENS 1964). Nevertheless, reduction in permeability and lowering of body fluid concentration point to the possibility that *M. gravelyi* is presently adjusting to freshwater life.

However advantageous these adaptations are in regard to life in brackish water, they are quite insufficient for existence in freshwater if they are not accompanied by corresponding changes in reproductive patterns (SMITH 1957). The provision of a jelly-coat to developing eggs and larvae as an effective barrier against changing environmental salinities (KRISHNAMOORTHI 1951), and the absence of a trochophore stage (AIYAR 1931) are, perhaps, two such adaptive changes in the reproductive patterns of *M. gravelyi*, that would help to establish a population in a fluctuating environment. Further evidence in support of our hypothesis is, perhaps, the geographical distribution of the genus *Marphysa*. As already discussed (KRISHNAMOORTHI 1963b), the genus *Marphysa* has a more cosmopolitan distribution than other species of polychaetes which co-exist with *M. gravelyi* in the Adyar estuary. Viewed against this background, the occurrence of *M. sanguinea* (ABBOT 1946) in a freshwater fishpond

(Wailupe Pond) is of great significance; it lends strong support to the assumption that *M. gravelyi* is likely to evolve towards a life in freshwater.

SUMMARY

1. The respiratory rate of body tissues of the polychaete *M. gravelyi* ranged from 3.13 μl/mg/hr to 6.34 μl/mg/hr in the four experimental salinities 10 ^{0}/oo, 14 ^{0}/oo, 17 ^{0}/oo and 24 ^{0}/oo. Since similar estimations in other polychaetes are not available in literature a comparison is difficult. However, the trends, i. e., increase of respiratory rates with increasing salinity, are similar to those reported for whole individuals of *N. diversicolor*.
2. In *M. gravelyi*, both the organic and inorganic ions are regulated. It is argued that the trend reported above may be traced to the operation of an effective ion transport system.
3. Two adaptations that may help to understand the trend of evolution in *M. gravelyi* are the reduction in permeability and the lowering of the body fluid concentration.
4. These two adaptations may indicate a tendency towards life in freshwater. A few other features, such as corresponding changes in the reproductive patterns of *M. gravelyi* and the geographical distribution of the genus *Marphysa* support this assumption.

LITERATURE CITED

ABBOT, D. P., 1946. Some polychaetous annelids from a Hawaiian fish pond. *Res. Publs Univ. Hawaii* **23**, 1–24.

AIYAR, R. G., 1931. An account of the development and breeding habits of a brackish water Polychaete worm of the genus *Marphysa*. *J. Linn. Soc.* **37**, 387–403.

— 1933. On the anatomy of *Marphysa gravelyi* Southern. *Rec. Indian Mus.* **35**, 287–323.

BEADLE, L. C., 1931. The effect of salinity changes on the water content and respiration of marine invertebrates. *J. exp. Biol.* **8**, 211–227.

— 1943. Osmotic regulation and the faunas of inland waters. *Biol. Rev.* **18**, 172–183.

— 1957. Comparative physiology: osmotic and ionic regulation in aquatic animals. *A. Rev. Physiol.* **19**, 329–358.

— & CRAGG, J. B., 1940a. Osmotic regulation in freshwater animals. *Nature, Lond.* **146**, 588.

— — 1940b. Studies on adaptation to salinity in *Gammarus* spp. 1. Regulation of blood and tissues and the problem of adaptation to freshwater. *J. exp. Biol.* **17**, 153–163.

BERTALANFFY, L., VON, 1951. Metabolic types and growth types. *Am. Nat.* **85**, 111–117.

— & KRYWIENCZYK, J., 1953. The surface rule in crustaceans. *Am. Nat.* **87**, 107–110.

BOSWORTH, H. W., O'BRIEN, H. & AMBERSON, W. R., 1936. Determination of the respiratory quotient in marine animals. *J. cell. comp. Physiol.* **9**, 77–87.

BRODY, S., 1945. Bioenergetics and growth. Reinhold, New York, 1023 pp.

CROGHAN, P. C., 1961. Competition and mechanisms of osmotic adaptation. *Symp. Soc. exp. Biol.* **15**, 156–167.

DEHNEL, P. A. & McCAUGHRAN, D., 1964. Gill tissue respiration in two species of estuarine crabs. *Comp. Biochem. Physiol.* **13**, 233–259.

DIXON, M., 1952. Manometric methods as applied to the measurement of cell respirations and other processes. Univ. pr., Cambridge, 166 pp.

ELTRINGHAM, S. K., 1965. The respiration of *Limnoria* (Isopoda) in relation to salinity. *J. mar. biol. Ass. U. K.* **45**, 145–152.

FLEMISTER, L. J. & FLEMISTER, S. C., 1951. Chloride ion regulation and oxygen consumption in the crab, *Ocypode albicans* (Bosq.). *Biol. Bull. mar. biol. Lab., Woods Hole* **101**, 259–273.

GROSS, W. J., 1957. An analysis of response to osmotic stress in selected decapod crustacea. *Biol. Bull. mar. biol. Lab., Woods Hole* **112**, 43–62.

KIRSCHNER, L. B., 1961. Thermodynamics and osmoregulation. *Nature, Lond.* **191**, 815–816.

KRISHNAMOORTHI, B., 1951. Studies on the osmotic properties of eggs, and larvae of a brackish water polychaete, *Marphysa gravelyi* Southern. *Proc. Indian Acad. Sci.* **34**, 199–209.

— 1963a. Chloride regulation in *Marphysa gravelyi* Southern. *Curr. Sci.* **32**, 463–464.

— 1963b. On the distribution of six species of polychaetes in the Adyar estuary, Madras. *J. mar. biol. Ass. India* **5**, 97–102.

— 1966. Physiological studies on *Marphysa gravelyi* Southern. 6. Regulation of total carbohydrates. (Submitted for publication.)

— & KRISHNASWAMY, S., 1965. Physiological studies ... 5. Regulation of chlorides, sodium, potassium and total free amino acids. *Helgoländer wiss. Meeresunters.* **12**, 315–328.

— — 1966a. Physiological studies ... 1. Salinity tolerance. *Proc. Indian Acad. Sci.* **63**, 26–34.

— — 1966b. Physiological studies ... 2. Volume regulation. *Proc. Indian Acad. Sci.* **63**, 117–125.

— — 1966c. Physiological studies ... 3. Regulation of body fluid concentration. *Zool. Jb. allgem. Zool. Physiol.* **72**, 316–326.

— — 1966d. Physiological studies ... 4. Structure of nephridia. (Unpublished.)

— — 1966e. Ionic regulation in *Marphysa gravelyi* Southern (Polychaeta). *Curr. Sci.* **35**, 72–73.

KROGH, A., 1939. Osmotic regulation in aquatic animals. Univ. pr., Cambridge, 1–242.

LOCKWOOD, A. P. M., 1961. "Ringer" solutions and some notes on the physiological basis of their ionic compositions. *Comp. Biochem. Physiol.* **2**, 241–289.

— 1962. The osmoregulation in crustacea. *Biol. Rev.* **37**, 257–308.

LOFTS, B., 1956. The effect of salinity changes on the respiratory rate of the prawn *Palaemonetes varians* (LEACH). *J. exp. Biol.* **33**, 730–736.

MARGARIA, R., 1931. The osmotic changes in some marine animals. *Proc. R. Soc.* (Ser. B) **107**, 606 ff.

PIEH, S., 1936. Über die Beziehungen zwischen Atmung, Osmoregulation und Hydration der Gewebe bei euryhalinen Meeresvertebraten. *Zool. Jb. (Allgem. Zool. Physiol. Tiere)* **56**, 129–160.

POTTS, W. T. W., 1954. The energetics of osmotic regulation in brackish and fresh water animals. *J. exp. Biol.* **31**, 618–630.

— & PARRY, G., 1964. Osmotic and ionic regulation in animals. Pergamon pr., New York, 423 pp.

SCHLIEPER, C., 1929a. Über die Einwirkung niederer Salzkonzentrationen auf marine Organismen. *Z. vergl. Physiol.* **9**, 478–514.

— 1929b. Neue Versuche über die Osmoregulation wasserlebender Tiere. *Sber. Ges. Beförd. ges. Naturw. Marburg* **64**, 143–156.

SCHWABE, E., 1933. Über die Osmoregulation verschiedener Krebse *(Malcostaceen)*. *Z. vergl. Physiol.* **19**, 183–235.

SMITH, R. I., 1957. A note on the tolerance of low salinities by nereid polychaetes and its relation to temperature and reproductive habit. *Année biol.* **33**, 93–107.

— 1959. Physiological and ecological problems of brackish-waters. *In:* Marine Biology. Proc. of the Twentieth Annual Biology Colloquium, Oregon State College. April, 1959, 50–69.

STEPHENS, G. C., 1964. Uptake of organic material by aquatic invertebrates. 3. Uptake of glycine by brackish water annelids. *Biol. Bull. mar. biol. Lab., Woods Hole* **126**, 156–162.

TARUSSOV, B., 1927. Über den Einfluß der osmotischen Bedingungen auf die Oxydationsgeschwindigkeit. *Zh. obshch. Biol.* **6**, 229 ff.

TOPPING, F. L. & FULLER, J. L., 1942. The accommodation of some marine invertebrates to reduced osmotic pressures. *Biol. Bull. mar. biol. Lab., Woods Hole* **82**, 372–384.

VERNBERG, F. J., 1956. Study of the oxygen consumption of excised tissues of certain marine decapod crustacea in relation to habitat. *Physiol. Zoöl.* **29**, 227–233.

WEYMOUTH, F. W., CRISMON, J. M., HALL, V. E., BELDING, H. S. & FIELD II, J., 1944. Total and tissue respiration in relation to body weight: a comparison of the kelp crab with other crustaceans and with mammals. *Physiol. Zoöl.* **17**, 50–71.

ZERAHAN, K., 1956. Oxygen consumption and active sodium transport in the isolated and short-circuited frog skin. *Acta physiol. scand.* **36**, 300–318.

ZEUTHEN, E., 1953. Oxygen uptake as related to body size in organisms. *Q. Rev. Biol.* **28**, 1–12.