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THE INFLUENCE OF ENVIRONMENTAL SALINITY ON THE WATER FLUXES OF THE AMPHIPOD CRUSTACEAN *GAMMARUS DUEBENI*

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It has been known for a number of years that removal of the eyestalks of decapod crustaceans disturbs the maintenance of the water balance of the animals during and after ecdysis (Scudamore, 1947; Carlisle, 1955; Passano & Jyssum, 1963; Bliss, Wang & Martinez, 1966). More recently it has been shown that ligaturing or removal of the eyestalks of crayfish (*Procambarus clarkii*) results in an increased urine output and this has been interpreted as indicating an increase in permeability to water at the body surface (Kamemoto & Ono, 1967). The semi-terrestrial crab *Metopograpsus messor* shows a similar effect (Kato & Kamemoto, 1969).

These results suggest that certain crustacea are able to vary the permeability of the body surface to water as has been found to occur in some species of euryhaline fish (Potts & Flemming, 1970; Motais, Isaia, Rankin & Maetz, 1969). Direct measurements of water flux in a range of salinities have not indicated, however, that all euryhaline crustacea vary their permeability to water. Smith (1967) has demonstrated that there is a decrease in the influx of D_2O into the crab *Rhithopanopaeus harrisi* when the animal was acclimatized to progressively more dilute media in the range 95 % sea water to 1 % sea water, and he also (Smith, 1970) showed a similar effect in *Carcinus maenas* over a somewhat smaller salinity range. In the prawn *Palaemonetes varians*, however, no such apparent change in permeability with salinity is present (Rudy, 1967).

As was recognized by Smith, variations in flux of D_2O or T_2O in different media do not necessarily imply that the animal is able to alter its permeability since such differences could also result if the transfer of water across the gills involved passage through pores or if unstirred layers are present on either the blood surface or medium surface of the epithelium. The manner in which pores could influence the flux of D_2O relative to the net transfer of water has been discussed by Koefoed-Johnsen & Ussing (1953) and by Ussing (1954), whilst Dainty & House (1966) have considered the way in which unstirred layers could account for the discrepancies sometimes observed between permeability coefficients calculated from flux data and those obtained from osmotic flow measurements. As a result of such interfering factors, comparison of the permeability coefficients derived from D_2O and T_2O measurements (P_{diff}) and those obtained by determination of net transfer of water down an osmotic gradient (P_{os}) usually give a ratio of P_{os}/P_{diff}, markedly in excess of one for tissues such as *Bufo regularis* skin (27·2), *Xenopus laevis* skin (9·3), *Rana esculenta* skin (10·1) (Maetz,

1968), where the surface is not actively irrigated. The corresponding ratio for the gills of the teleost fish *Anguilla* and *Platichthys* are respectively 3·16 and 2·59 when the animals are acclimatized to fresh water and 1·05 and 0·83 when they are in sea water (Motais, Isaia, Rankin & Maetz, 1969). The ratio P_{os}/P_{diff} is thus closer to unity in fish than in amphibian skins, but since the value does not remain constant in different media it is clearly impracticable to rely upon D_2O or T_2O fluxes alone as indicating variations in permeability. By measuring urine volumes and drinking rates Motais *et al.* (1969) were, however, able to demonstrate unequivocably that *Anguilla* and *Platichthys* increase their permeability to water when acclimatized to fresh water.

The position in the case of brackish-water crustacea is less certain, though the work of Smith (1967, 1970) coupled with that of Kato & Kamemoto (1969) implies that some crabs show some decrease in permeability when in dilute media.

The amphipod *Gammarus duebeni* has blood which is almost isosmotic with the medium when the animal is in sea water (Beadle & Cragg, 1940; Haywood, 1970). When in this medium the rate of active sodium transport into the animal is increased both when the animal moults and when the body volume is caused to fall in intermoult animals. These findings have been interpreted as indicating that water uptake to expand the body after ecdysis and water uptake to replace fluid loss occur in association with an active uptake of ions when the animals are isotonic with their media (Lockwood & Andrews, 1969; Lockwood, 1970). Since this animal also maintains itself hypertonic to the media when in media less concentrated than 50% sea water, there is a strong implication that it must be able to vary the permeability of the body surface to water independently of the permeability to inorganic ions. Such a variation in the relative permeability to ions and water in different media has already been demonstrated in the annelid *Nereis diversicolor* (Smith, 1964).

Variations in the permeability of intermoult *Gammarus duebeni* in relation to salinity are studied in the present paper.

MATERIAL AND METHODS

Animals

Gammarus duebeni were obtained from the salt marshes at Redbridge on the River Test and maintained, prior to experimental acclimatization, in 50% sea water. They were fed during this period on *Enteromorpha* and 'Bemax'.

Experimental animals were acclimatized to appropriate medium for at least 4 days prior to measurement.

Exchange rates may be influenced by the size of the animal, so as far as possible animals of similar size were used. Usually the weight range lay within 60–90 mg.

Flux experiments

Water fluxes were measured in both directions, influx and outflux, by means of ^3H_2O. The vessels holding the animals were closed during the experiments to prevent loss of tritium by exchange with water vapour in the air. For outflux measurements animals were transferred to a tritiated water solution of the same salinity as the acclimatization medium and left to load for approximately 10 half-times (2 h). They were rinsed briefly in unlabelled medium and transferred to 10 ml of unlabelled

medium in a capped vessel. Aliquots (50 μl) of this medium were taken at frequent intervals for about $\frac{1}{2}$ h. Double aliquots were taken after several hours to establish the terminal level of count.

The flux, as a percentage of body water/minute, was calculated from 100 (ln $2/t_{\frac{1}{2}}$), where $t_{\frac{1}{2}}$ is the time for half exchange of the body water.

Net osmotic flow

Putative osmotic water flow was calculated from flux data on the basis of the differences in mole fraction* of water in the medium and in the blood of the animal.

$$\left(\frac{M_m - M_a}{M_m}\right) f = O_s$$

where M_m is the mole fraction of water in the medium, M_a is the mole fraction of water in the blood, f is the water flux and O_s is the osmotic water flow.

Tritium counts were made by pipetting 50 μl aliquots of medium into 4 ml of Dioxane-based phosphor (Naphthalene, POPOP and PPO) and determining the activity in a Panax liquid scintillation counter. Tests indicated that quenching effects due to variations in the salinity of the medium are negligible.

Electron microscopy

Animals from 100% and 2% sea water were killed and the gills were removed and fixed in glutaraldehyde. These were blocked in Araldite, sectioned at *ca.* 200 Å, stained with uranyl acetate and lead citrate and examined by means of a Phillips 300 electron microscope.

RESULTS

Water flux in relation to the salinity of the medium

Outflux

Animals previously acclimatized to salinities in the range 2–100% sea water were placed in tritiated solutions of the same salinity until they reached isotopic equilibrium (*ca.* 10 half-times for exchange), and then after a brief rinse were transferred to 10 ml of unlabelled medium to unload. Aliquots of the medium were counted at intervals until a steady state was reached.

Semi-logarithmic plots of the loss against time gave a straight line (Text-fig. 1) indicating that the exchange is effectively governed by a single rate constant.

Measurements of the exchange in different salinities showed, despite considerable individual variation, that the apparent permeability to water (as based on the half-time for exchange) is about twice as great when the animals are in salinities in the range 75–150% sea water as it is in salinities of 50% sea water and lower concentrations (Text-fig. 2).

In general, most of the change in apparent permeability occurs in the ranges 50–75% sea water.

Measurements of water flux made when an osmotic gradient is present between

* Mole fraction is taken as $55{\cdot}556/(55{\cdot}556+x)$, where x is the osmolal concentration.

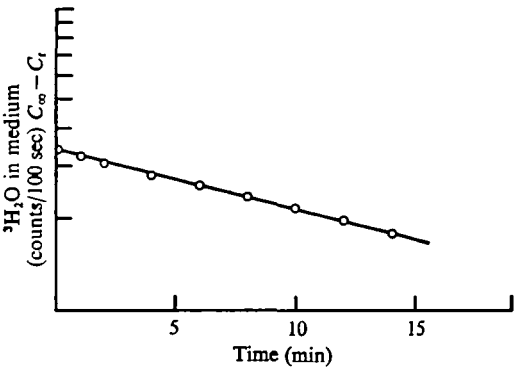

Fig. 1

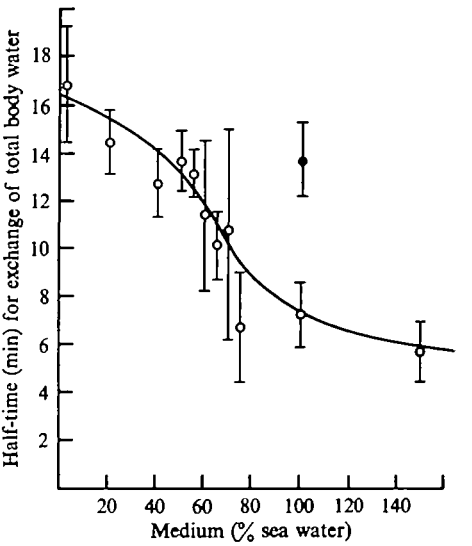

Fig. 2

Fig. 1. Semi-logarithmic plot of increasing count of medium against time showing that water outflux is governed by a single rate constant.

Fig. 2. The relationship between the concentration of the medium and water flux. ●, Isosmotic mannitol; ○, saline media.

blood and medium cannot be used with confidence for calculation of water uptake by osmosis since they are liable to errors caused *inter alia* by bulk flow of fluid across the membrane (Motais *et al.* 1969). Possible sources of error from this cause were investigated by comparing the values for influx of tritiated water with the values for outflux.

Influx

Influx measurements were made by placing weighed animals in tritiated water at various salinities for a period of exactly 5 min, then, after blotting them dry, allowing them to exchange to a steady state in 10 ml of unlabelled medium. After this period of unloading, the same animals were loaded to a steady state in the original tritiated medium and once more completely unloaded in 10 ml of unlabelled medium. The percentage of the saturation count achieved in the 5 min period of exposure was then calculated from the count of aliquots of the 10 ml samples.

Half-times of exchange in animals acclimatized to 100% sea water and 2% sea water were respectively $5{\cdot}5 \pm 1{\cdot}3$ min ($N = 12$) and $17{\cdot}6 \pm 2{\cdot}6$ min ($N = 5$), as compared with the outflux values of $7{\cdot}3 \pm 1{\cdot}4$ min ($N = 16$) and $16{\cdot}8 \pm 2{\cdot}5$ min ($N = 16$).

The outflux and influx measurements are thus not significantly different in the case of animals from 2% sea water.

The time course of apparent permeability change

In view of the suggestion by Mantel (1967) and Kamemoto & Ono (1967) that hormones may influence the movement of water into crustacea, the time course of the apparent permeability change in *Gammarus* has been investigated.

The influx into animals previously acclimatized to 100% sea water was measured

Table 1. *Time course of apparent permeability change*

	0 h 100/100*	16 h 2/2	40 h 2/2	64 h 2/2
$t_{\frac{1}{2}}$ (min)	3·9	12·7	13·2	12·5
σ	±0·6	±4·0	±2·7	±3·0
N	10	10	10	10

* The paired values below the times are the concentration of sea water (as a percentage) of the media in which the animals had been acclimatized (left-hand value) and that in which it was unloaded (right-hand value).

Table 2. *Summary of influx and outflux data*

Acclimatization salinity % SW	Test medium % SW	Direction	$t_{\frac{1}{2}}$ (min)	σ	No.
150	150	Outflux	5·8	±1·3	3
100	100	Outflux	7·3	±1·40	16
75	75	Outflux	6·75	±2·32	6
70	70	Outflux	10·87	±4·26	6
65	65	Outflux	10·15	±1·44	6
60	60	Outflux	11·40	±3·28	6
55	55	Outflux	13·13	±1·02	6
50	50	Outflux	13·68	±1·21	6
40	40	Outflux	12·75	±1·49	12
20	20	Outflux	14·47	±1·40	3
2	2	Outflux	16·8	±2·5	16
100	50	Outflux	13·5	±2·0	12
2	50	Outflux	12·2	±3·1	12
2	100	Outflux	22·2	±5·1	12
100	100	Influx	5·5	±1·3	12
2	2	Influx	17·6	±2·6	5

in 100% sea water and they were then transferred to 2% sea water for 16 h. After this period the influx was measured in 2% sea water. Repeat measurements of influx in 2% sea water were made after 40 and 64 h. The results (Table 1) indicated that the change in apparent permeability had occurred within the first 16 h after the transfer to 2% sea water.

A supplementary experiment was carried out in which the acclimatization period in 2% sea water before the initial measurement in this medium was reduced from 16 to 2 h. Nevertheless, a similar result was found, the half time for exchange in 100% sea water being 7·0 min, and after 2, 26 and 50 h in 2% sea water being respectively 16·8, 13·7 and 15·7 min. Since this latter experiment indicates that the apparent permeability change occurs with some rapidity, a test was made of the effect of direct transfer of animal from 100% sea water to 50% sea water followed by immediate measurement of outflux in the latter medium (Table 2). The $t_{\frac{1}{2}}$ was closely similar to that for fully acclimatized animals in 50% sea water, and since a semilogarithmic plot of the count of the media against time is a straight line there must be a strong presumption that the change in apparent permeability occurs almost instantaneously on an alteration of the concentration of the medium.

The converse experiment, involving transfer of animals from 2% to 100% sea water, produced a somewhat unexpected result. In this case, instead of the apparent permeability increasing at once to the level found in sea water, it initially decreased

Table 3. *Half-time for water exchange at various periods after transfer of animals from 2% sea water to 100% sea water*

(Time since transfer to 100% sea water (h) from 2% sea water.)

$t_{\frac{1}{2}}$ (min)	Half-time for influx in 2% sea water	16 100/100	40 100/100	64 100/100
Mean	12·1	8·3	6·0	6·1
σ	±1·8	±2·5	±1·5	±1·6
N	10	10	10	10

Table 4. *Outflux of water in animals transferred from 2 to 50% sea water*

$t_{\frac{1}{2}}$ (min)	After direct transfer	After acclimatization
Mean	12·1	13·7
σ	±3·1	±1·2
N	12	6

still further. Thus the half-time for outflux in animals transferred directly from 2% sea water to 100% sea water and measured immediately was 22·2 ± 5·1 min as opposed to the value of 7·3 ± 1·4 min for outflux in animals fully acclimatized to sea water and 16·8 ± 2·5 for animals fully acclimatized to 2% sea water. This decrease in the flux rate on transfer to a salinity hypertonic to the blood is temporary only but nevertheless lasts at least 2 h, since an individual, previously acclimatized to 2% sea water, whose outflux was tested in 2% sea water and then after 2, 26 and 50 h in 100% sea water had respective half times for outflux of 19·0, 26·2, 6·1 and 6·3 min. The influx, however, is approaching the level found in fully acclimatized animals within 16 h after transfer from 2% to 100% sea water. When influx was tested before transfer and at 16, 40, 64 and 88 h after transfer to 100% sea water the values given in Table 3 were obtained.

The value at 16 h is tending towards that in the 40 and 64 h experiments but both the difference and the wider standard deviation of results suggest that the steady-state condition has not been fully established at this time. It is perhaps also worth stressing that since one of these experiments was of the influx and another of outflux the flux in both directions is affected initially by the change from 2% to 100% sea water.

By contrast with the above results, animals transferred from 2% sea water to 50% sea water (with which the blood is approximately isosmotic initially) show neither a transitory (within 2 h) nor longer-term change in apparent permeability. Table 4 indicates in fact the close similarity of outflux values obtained in animals following direct transfer from 2% to 50% sea water and those fully acclimatized to 50% sea water.

Water flux in relation to non-ionic osmotic concentration of the medium

Additional experiments were undertaken to test whether the variations in apparent permeability noted above were correlated with the osmotic concentration *per se* or with the ion concentration of the medium.

Animals previously acclimatized to 100% sea water were loaded in tritiated sea water and then transferred, after a quick rinse in unlabelled sea water, to an isotonic mannitol solution (16·7 g, plus 100 ml de-ionized water) into which the outflux was measured. The half-time values for outflux obtained ($13{\cdot}7 \pm 1{\cdot}5$ min, $N = 6$) were more like those observed when *Gammarus duebeni* is acclimatized to 2% sea water and its outflux measured into 2% sea water ($16{\cdot}8 \pm 2{\cdot}5$ min, $N = 16$) and differed markedly from outflux measurements into sea water with which the mannitol was isotonic ($7{\cdot}3 \pm 1{\cdot}4$ min, $N = 16$). A semi-logarithmic plot of the activity within the animals against time gave a straight line, indicating that the apparent permeability was not changing during the period from 1 min after transfer to the mannitol solution to 30 min later. Since the half-times measured over the period approximate to the levels found in animals acclimatized to 2% sea water rather than to those in 100% sea water it appears (*a*) that the change in apparent permeability takes place virtually instantaneously on transfer to the mannitol solution and (*b*) that the osmotic pressure of the medium is less important than the ionic concentration in determining the apparent permeability of the animals to water.

In order to determine whether the marked increase in the half-time for water exchange on transfer of animals from 2% sea water to 100% sea water was due to an osmotic effect on fluid movement or to some other parameter, animals from 2% sea water were loaded in this medium and then transferred directly to a mannitol solution isotonic with 100% sea water. The half-time of outflux showed no indication of the marked decrease shown on transfer to 100% sea water. Again therefore it appears that an ionic effect rather than an osmotic effect is involved.

DISCUSSION

The experiments described above and summarized in Table 5 indicate that considerable variations in the fluxes of water can occur across the body surface of *Gammarus duebeni* when the animal is acclimatized to different salinities or transferred from one salinity to another. Similar, though somewhat smaller, flux variations in relation to the salinity of the medium have been observed by Smith (1967, 1970) working on the crabs *Rhithopanopaeus harisi* and *Carcinus maenas*, though no such changes occur in the prawn *Palaemonetes varians* (Rudy, 1967).

Euryhaline animals might derive some energetic advantage if able to adjust their permeability to ions and water as the osmotic gradient between blood and medium varies. It is tempting therefore to correlate the decrease in water flux which occurs when *G. duebeni* is acclimatized to media below 50% sea water with the fact that the blood becomes markedly hypertonic to the medium at salinities lower than this. However, as has been repeatedly pointed out (Dainty & House, 1966, Motais, Isaia, Rankin & Maetz, 1969; Smith, 1970) changes in flux could arise as artifacts through changes in unstirred layers on either side of the water-permeable membranes or as a result of bulk flow through pores interfering with diffusional exchange without true permeability changes being involved. Smith (1970) therefore advisedly discussed the flux changes he observed in terms of 'apparent permeability changes'. Since only an actual change in permeability would be of physiological significance to the animal it is necessary to consider whether the flux changes observed in *Gammarus* (Fig. 2) are indicative of genuine or of only apparent variations in permeability.

A priori it would appear unlikely that the unstirred layers would increase in thickness (and hence slow the apparent water exchange) if the salinity of the media is decreased, since Kinne (1952) has shown both that the heart rate is greater and the oxygen consumption larger in *G. duebeni* in dilute media than at high concentrations. Neither blood flow through nor respiratory flow past the gills, which may respectively be expected to influence any superficial unstirred layers on either face of the epithelial cells of the gill, would therefore be likely to be less in low than in high salinities. Such an argument would not of course rule out the possibility that morphological changes at the subcellular level would alter the size of unstirred layers, and in this context the variation in structure of certain epithelial cells must be considered. Copeland & Fitzjarrel (1968) have shown that when the crab *Callinectes* is in dilute media the subcuticular surface of the epithelial cells of the gills has the form of lamellar folds terminating in finger-like processes which contact the cuticle. These folds are separated from each other by relatively large spaces. The gills of the freshwater amphipod *Gammarus pulex* show similar structures (P. Whitfield, unpublished). By contrast, in *Ligia oceanica* from sea water the lamellae are broader and in consequence the interlamella spaces are reduced to narrow channels (Sylvester, 1970).

In *Gammarus duebeni* the structure approximates to that found in the marine species when the animal is in 100% sea water but shows the same form as that in *G. pulex* when it is in 2% sea water (Pls. 1 and 2). The physiological significance of this structural variation in relation to the salinity of the medium is not yet clear but the different anatomical form at high and low salinities could, in theory, contribute to the observed flux differences in 100% sea water and 2% sea water by varying the extent of unstirred layers beneath the cuticle. Thus it could be argued that when animals are in sea water and much of the cell surface is closely applied to the cuticle, there is a shorter pathway for water movement than in the 2% sea water condition when relatively large fluid pools separate the bulk of the cell surface from the media external to cuticle.

In view of this the intra-lamellar pools might be seen as forming unstirred layers whose presence is responsible for the apparent decrease in water flux when the animals are in dilute media. However, there is circumstantial evidence which suggests that the observed decrease in flux is not solely due to an experimental artifact but that there is also at least some degree of actual decrease in permeability to water.

Measurements of the urine flow rate of *Gammarus duebeni* acclimatized to 2% sea water have produced a value (Lockwood & Inman, 1972) that is closely similar to the theoretical urine volume expected on the basis of the water flux and fraction difference between the blood and media. Thus the urine flow rate obtained by clearance studies of sodium diatrizoate was 50·2% of the body weight/day whilst the value obtained from the flux studies was 54·0% body weight/day. The ratio of these two functions of the permeability coefficients (fP_{os}/fP_{diff}) is close to unity implying that the flux data represents the actual diffusional water exchange at the body surface and that there is no gross interference with free diffusional exchange. In tissues where there is interference with free diffusion the ratio fP_{os}/fP_{diff} would be expected to differ more widely from unity. If there is indeed no interference with diffusional passage of water across the gills in 2% sea water then it would follow that the greater permeability of the animals when in sea water represents a genuine permeability difference.

Table 5. *The potential difference across the body wall of intermoult* Gammarus duebeni, *and of animals in the first day after moult, following transfer from* 100% *sea water to other media*

(All values millivolts; the sign of the potential is that of the blood with respect to the medium.)

Intermoult	Sea water	2% sea water	De-ionized water	Sucrose isotonic with 100% SW
Mean	−4·5	−11·8	−28·7	−8·7
Range	−2·5 to −7·5	−4·5 to −19·5	−6·6 to −64·4	−1·3 to −25·5
N	8	8	8	8
First day after moult				
Mean	−7·1	−33·5	−42·7	−25·8
Range	−2·6 to −15·1	−23·9 to −41·7	−29·3 to −55·3	−6·7 to −35·6
N	4	4	4	4

Two features of interest in the flux change are (1) that much of the change seems to occur in most animals over the relatively narrow salinity range from 50 to 75% sea water, and (2) that like *Rhithopanopaeus* and *Carcinus* (Smith, 1967, 1970) *Gammarus* shows a reduced permeability in low salinities, whereas the change is in the opposite direction in the euryhaline fish *Tilapia* (Potts *et al.* 1967; Evans, 1969).

In fish Potts & Fleming (1970) have shown that both the hormone prolactin and $[Ca^{2+}]$ influence the permeability of the body surface. Kato & Kamemoto (1969) have also suggested that hormonal control of the body-surface permeability occurs in decapod crustacea. However, it is unlikely that either $[Ca^{2+}]$ or hormones are responsible for the flux variations at different salinities reported here for *Gammarus* since (*a*) the virtually instantaneous flux change which follows transfer of *G. duebeni* from 100% sea water to isotonic mannitol or dilute salinities seems to preclude the action of a hormonal system, whilst (*b*) the fact that (unlike the condition in fish) the flux declines in solutions with low, or no Ca^{2+} seems to indicate that this factor is not of importance. The observation of Bialawski (1964) that *isolated* crayfish gills also show a decrease in water permeability as the gradient between blood and media is decreased also argues against the probability of universal hormonal control of permeability.

The factor responsible for the flux change remains uncertain. It would not appear to be related to the osmotic concentration of the medium since transfer from 100% sea water to a mannitol solution isotonic with sea water produces a flux change (Table 2). Nor does it appear to be associated with bulk flow of fluid across the surface since transfer of animals from 2% sea water to 100% sea water causes a large initial decrease in flux whereas no such change occurs when transfer is made from 2% sea water to mannitol isotonic with 100% sea water.

If neither the osmotic gradient nor the absolute osmotic concentration is responsible for determining the flux it would seem plausible to consider the possibility that either the concentration of an individual ion or the magnitude of the potential across the body surface may play some role. Measurements of the potential made in different media (Table 5) and by Lockwood and Andrews (1970) indicate that the potential increases somewhat as the medium is diluted and in isotonic non-electrolyte. Superficially therefore it would seem that a case might be made for relating the rapid

changes in water flux which occur on transfer from one media to another with the corresponding variations in trans-epithelial potential which would be a consequence of such a salinity change. Against such a postulate, however, is the observation that both water fluxes and trans-epithelial potential increase in freshly moulted animals (Lockwood & Inman, 1972), whereas if there were any direct inter-relationship between the magnitude of the potential and the water flux the flux should decrease with increase in potential.

No information is available about direct effect of ions or of any possible nervous control of permeability in these animals, and in the present meagre state of knowledge further speculation on the possible means by which the permeability change could be effected would be pointless.

Irrespective of the means by which permeability changes are brought about, the end result could be of physiological advantage to the animal. In most crustacea so far studied the urinary loss of ions constitutes only about 10% of the total loss (*Eriocheir sinensis* 14%, Krogh, 1938; *Austropotamobius* 8–10%, Shaw, 1959, Bryan, 1960; *Potamon*, Shaw, 1959). In *Gammarus duebeni*, however, the ion loss in the urine contributes a much greater proportion of the total loss (Lockwood, 1965; Sutcliffe, 1967). Reduction in water permeability and the consequent decrease in urine volume when the animal is in dilute media would therefore effect some conservation of inorganic ions and hence confer an energetic advantage. It is of interest in this connexion that the change in water permeability usually occurs in the range 75–50% sea water, similar to the concentration at which the animals' blood begins to be maintained noticeably hypertonic to the medium (Beadle & Cragg, 1940). Similarly it could be argued that the ability to increase the permeability of the body surface to water might be advantageous when the animals are isotonic with their media if they are then dependent on some form of ion-driven water transfer for obtaining the fluid necessary for urine production. Increased permeability in such circumstances could perhaps permit a more rapid fluid uptake. This question is discussed in more detail by Lockwood & Inman (1972).

SUMMARY

1. The effect of salinity on the apparent permeability to water of *Gammarus duebeni* has been studied.

2. The apparent permeability when the animals are acclimatized to sea water or 150% sea water is more than twice that when they are in dilute media. The change from the level of permeability found in sea water to that in dilute media occurs largely in the range 75–50% sea water.

3. Permeability change occurs within 5 min when animals acclimatized to sea water are transferred to dilute media.

4. When animals from sea water are transferred to a mannitol solution isotonic with sea water the permeability changes to a level close to that found in animals in dilute salines.

5. This last observation is taken to indicate that the stimulus initiating the change in apparent permeability is not an osmotic one. Other possibilities are discussed and the value to the animals of changes in its permeability to water are considered.

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EXPLANATION OF PLATES

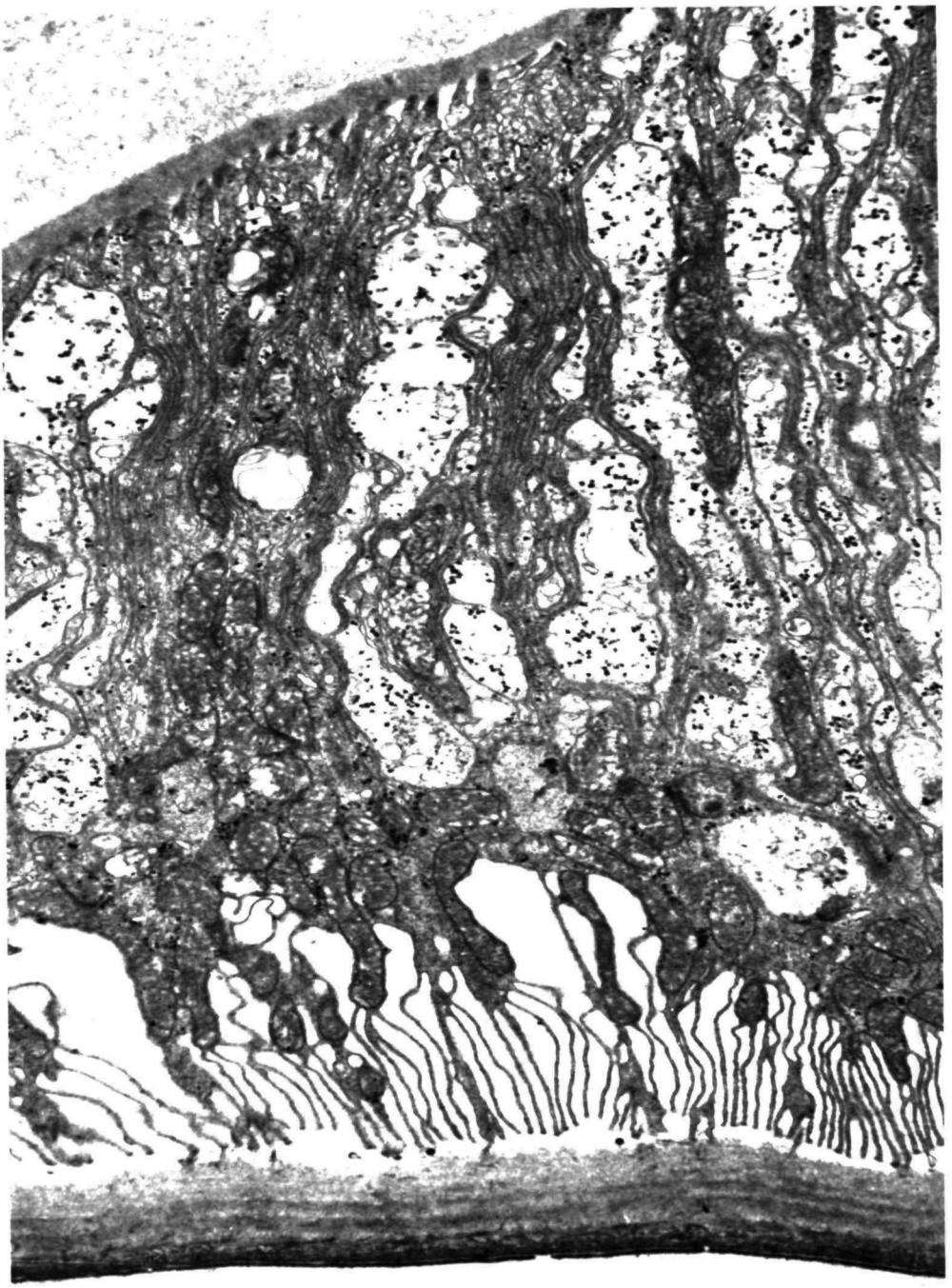
PLATE 1

General view of a transverse section of gill epithelium from *Gammarus duebeni* from 2% sea water. Gill blood sinus top left, cuticle at bottom of picture. × 12000.

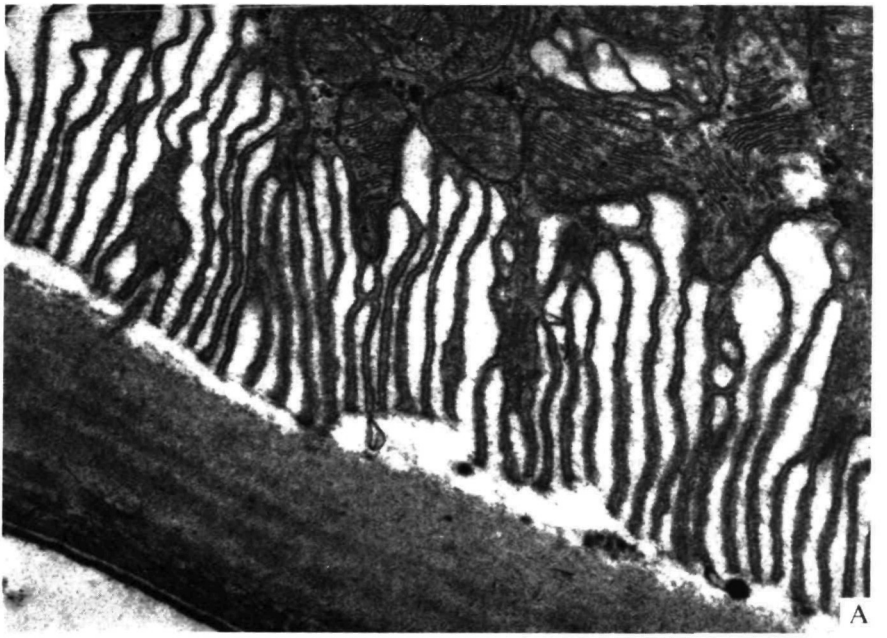
PLATE 2

(A) Distal portion of a gill epithelial cell from an animal acclimatized to 2% sea water showing the subcuticular lamellae and large inter-lamellar spaces. × 30000.

(B) Distal portion of a gill epithelial cell from an animal acclimatized to 100% sea water showing subcuticular inter-lamellar spaces reduced to narrow channels. × 30000.



A. P. M. LOCKWOOD, C. B. E. INMAN AND T. H. COURTENAY (*Facing p.* 148)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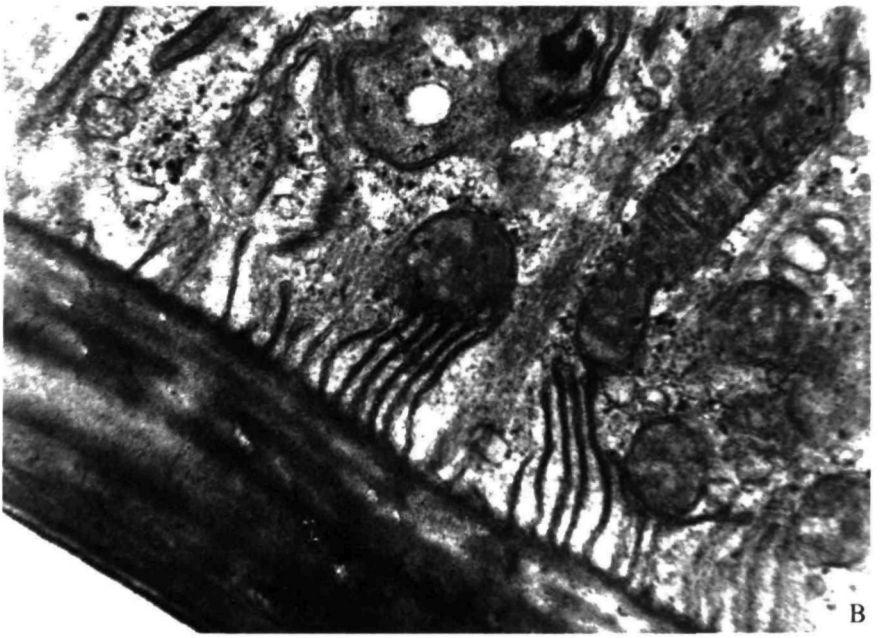
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