

## WATER PERMEABILITY OF *PALAEEMON LONGIROSTRIS* AND OTHER EURYHALINE CARIDEAN PRAWNS

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### Summary

Water permeability [based on the half-time of exchange of body water with the environment ( $T_{1/2}$ )] of the upper estuarine prawn *Palaemon longirostris* was measured in a range of salinities at 4, 12 and 20°C. Prawns acclimated for 7 days were compared with prawns exposed to acute salinity changes. Acclimation to low salinity and low temperature caused a significant reduction in permeability. Transfer of prawns from 34 to 0.5‰ had no immediate effect on permeability; however, transfer from 0.5 to 34‰ caused an immediate significant rise in permeability. Heart rate of *P. longirostris* acclimated to 0.5 and 34‰ at 4, 12 and 20°C was unaffected by salinity, but was significantly reduced at low temperature.

The permeabilities of three other prawn species (*Palaemonetes varians*, *Crangon crangon* and *Palaemon elegans*), which have different horizontal distributions in estuaries and different salinity tolerance ranges, were also studied and compared with the values obtained for *P. longirostris*. *P. varians* and *C. crangon* showed significantly reduced permeabilities at low compared with high salinities; however, the permeability of *P. elegans* was unchanged at the two salinities used for this species (22 and 34‰). At each experimental salinity, permeabilities followed the sequence: *P. longirostris* < *P. varians* < *C. crangon* < *P. elegans*. Results show that reduction of permeability is an important physiological adaptation to life in dilute saline regions and may be involved in separating species with overlapping salinity tolerance ranges.

### Introduction

Crustaceans living in hypo-osmotic environments lose salts and gain water, but have physiological mechanisms that compensate for these exchanges and maintain hyperosmotic body fluids (Gilles, 1975; Kirschner, 1979; Mantel and Farmer, 1983; Greenaway, 1979; Spaargaren, 1979). Rates of water gain and salt loss may be limited by lowering the permeability of the body surface (Lockwood, 1976), and there is a general trend amongst crustaceans of a less permeable body surface as the osmotic gradient between the body fluids and the external medium increases (Potts and Parry, 1964; Rudy, 1967; Bolt, 1983, 1989). Indeed, reduction of

**Key words:** water permeability, salinity, temperature, *Palaemon longirostris*, *Palaemonetes varians*, *Crangon crangon*, *Palaemon elegans*, habitat.

surface permeability is considered to be a major adaptation to life away from the sea. Animals living under conditions of fluctuating salinity would also clearly benefit from an ability to alter surface permeability, and such flexibility would require a mechanism sensitive to the concentration between the blood and the external medium (Bolt, 1983). Examples of euryhaline crustaceans with this ability are limited but include the crabs *Carcinus maenas* (Smith, 1970), *Rhithropanopeus harrisi* (Smith, 1967) and *Hemigrapsus nudus* (Smith and Rudy, 1972) and the amphipods *Gammarus duebeni* (Lockwood and Inman, 1973; Bolt *et al.* 1980; Bolt, 1983) and *Corophium voluinator* (Taylor, 1985).

*Palaemon longirostris* (Milne Edwards) occupies the upper, dilute saline regions of large river estuaries (Smaldon, 1979). It has a salinity tolerance range between 0.5 and 43‰ (Campbell and Jones, 1990) and maintains almost constant haemolymph osmotic and ionic concentrations over this wide salinity range (Campbell and Jones, 1989*a,b*). The present study investigates the changes in water permeability of *P. longirostris* acclimated to different salinities and exposed to sudden salinity change. Since temperature affects the osmotic and ionic regulation of *P. longirostris* (Campbell and Jones, 1989*a,b*), the influence of temperature on the water permeability of *P. longirostris* is reported also. The permeabilities of three other prawn species [*Palaemonetes varians* (Leach), *Crangon crangon* (Linnaeus) and *Palaemon elegans* (Rathke)] were studied and compared with the observations on *P. longirostris*. All are euryhaline but they have different salinity tolerance ranges and habitats. *P. varians* occurs in brackish-water pools indirectly connected to the sea and tolerates salinities between 1 and 30‰ (Hagerman and Uglow, 1983). *C. crangon* occupies the lower reaches of estuaries and tolerates salinities between 5 and 39‰ (Broekema, 1941). *P. elegans* is essentially an intertidal species and has a salinity tolerance range between 5 and 45‰ (Ramirez de Isla Hernandez and Taylor, 1985).

## Materials and methods

### *Animal husbandry*

All these prawn species occur within the River Tamar Estuary, Plymouth, but in different regions. *Palaemon longirostris* were collected from the upper reaches at Calstock, *Crangon crangon* from the lower reaches at Cargreen and *Palaemonetes varians* from brackish-water pools at St Johns Lake. *Palaemon elegans* occurs around the estuary mouth but, as access to suitable sites was limited, prawns were taken from intertidal rockpools at Wembury. They were hand-netted at low tide and transported back to the laboratory in habitat water. They were maintained in plastic aquaria supplied with continuously flowing sea water (salinity 34‰; temperature 12°C) and fed once a week on mussel (*Mytilus edulis* L.) or fish (*Gadus* sp.). For each species, 10 intermoult prawns of carapace length 18–24 mm (measured from rostral tip to posterior carapace edge) were acclimated for 7 days to an experimental salinity at 4, 12 or 20°C (to  $\pm 1^\circ\text{C}$ ) (temperature was controlled with the use of constant-temperature water baths). Prawns were held in plastic

aquaria (50 l) supplied with continuously aerated, recycled water at the appropriate salinity and temperature. They were subjected to a 12 h light:12 h dark cycle, and were not fed for 3 days prior to or during the experiments.

#### *Steady-state salinity experiments*

Permeability was determined by measuring the time taken for half the body water to exchange with the external medium ( $T_{1/2}$ ), using tritiated water (THO) as a tracer (Lockwood *et al.* 1973). This method of determining water permeability has certain limitations since it does not take into account either boundary layer resistance (both inside and outside the animal) or bulk flow through pores (Lockwood *et al.* 1973). For these reasons, the term 'apparent water permeability' (AWP) is used when referring to permeability determined by the THO outflux technique (Smith, 1967). Tests by Bolt (1983), however, have shown that measurements of  $T_{1/2}$  using THO were comparable to those based on direct urine measurements, suggesting that changes in water permeability using THO as a marker do reflect real changes in the water permeability of an animal.

Water permeability of *Palaemon longirostris* was measured at 12°C in 0.5, 7.0, 22.0, 34.0 and 43.0‰, and at 4 and 20°C in 0.5 and 34‰. Water permeability was also determined at 12°C for *Palaemonetes varians* in 0.5 and 34‰, *Crangon crangon* in 7, 22 and 34‰ and *Palaemon elegans* in 22 and 34‰.

Prawns were transferred from the acclimation aquaria to screw-top glass jars containing 250 ml of THO ( $50 \mu\text{Ci ml}^{-1}$ ) of the same salinity and temperature as in the acclimation medium and left to load for a minimum period of 5 h. They were then removed and thoroughly rinsed with 600 ml of water of the appropriate salinity and temperature. Prawns were subsequently blotted dry with absorbent tissue and transferred to a blank unloading medium containing 250 ml of water at the same salinity and temperature as the loading medium. This unloading medium was contained within screw-top jars to prevent any exchange of THO with water vapour in the air. The time of immersion in the unloading medium was noted and 100  $\mu\text{l}$  samples were taken 2, 4, 8, 16, 32 and 64 min after immersion ( $C_t$ ). The samples were placed into 4 ml of a liquid scintillation cocktail (cocktail 'Ex' Scintran, BDH) and counted using a liquid scintillation counter (Philips, model PW 4700). Tests by Lockwood *et al.* (1973) showed that quenching of the counts due to differences in the salinity of the external medium were negligible. The last sample was taken when the THO in the animal was in equilibrium with the external medium ( $C_\infty$ ) and this is equivalent to more than  $10 \times T_{1/2}$ .  $\log(C_\infty - C_t)$  was plotted against time and, if the permeability was constant throughout the experiment, the result was a straight line. Using a regression line fitted to the data, the time taken for half the body water to be exchanged with the external medium ( $T_{1/2}$ ) was calculated by taking the  $x$  value of the  $y$  point corresponding to  $\log C_\infty - \log 2$ . The correlation coefficient of the straight line was generally greater than 0.98, so only two  $C_t$  values needed to be taken at a time close to that of the  $T_{1/2}$  to fit a regression line to the data. This short cut, however, could only be

taken when the approximate  $T_{1/2}$  was known (e.g. when experiments were replicated for prawns at the same salinity/temperature combination).

#### *Sudden salinity transfer*

Changes in permeability of *Palaemon longirostris* acclimated for 7 days to 34 and 0.5 ‰, and transferred directly to 0.5 and 34 ‰, respectively, were measured in 10 prawns at 12°C. Water permeability was determined by measuring the  $T_{1/2}$  for THO outflux using the same method as described in the previous section, except that prawns loaded in 34 ‰ were unloaded in 0.5 ‰ and *vice versa*.

#### *Heart rate in Palaemon longirostris*

The heart rates of five prawns acclimated to each combination of salinity (0.5 and 34 ‰) and temperature (4, 12 and 20°C) were measured using an impedance technique (Johnson, 1985). Two impedance pneumograph transducers (Classic H7, Scientific Instruments Centre) were coupled to a two-channel oscillograph (George Washington Ltd). A small pin (recording) electrode was implanted close to the pericardium and a large common earth electrode was placed in the tank containing the prawn; both electrodes were connected to a single transducer. The pneumograph produced a small oscillating current between the two electrodes, and any movements occurring close to the pin electrode (e.g. heart beat) were detected, filtered and amplified. The output of each transducer was recorded on a chart recorder, so that a quantitative analysis of the heart rate could be carried out.

For each prawn, the carapace was dried thoroughly with absorbent tissue and the recording electrode (made from 0.25 mm plastic-coated miniature solid wire, which had the last 4 mm bared and bent through 180°) was inserted between the carapace and the first abdominal segment. Care was taken not to puncture the arthroal membrane and the electrode was placed close to the pericardium. The wire attached to the electrode was bent back and anchored to the carapace using a combination of super glue and a low melting point wax. Animals were returned to the aquarium as soon as the wax had dried. This technique was based on that originally described by Dyer and Uglow (1977).

Prawns with attached electrodes were separated by plastic dividers and held at the appropriate salinity in covered plastic aerated aquaria (volume=2.5 l). Aquaria were covered to prevent any shadow stimulating heart rate. After electrode attachment, the prawns were left to recover for 24 h before readings were taken, thereby enabling the heart rate to return to a non-stressed level (Cumbridge and Uglow, 1977). A recording of heart rate from each prawn was taken for approximately 2 min.

#### *Statistical analysis*

Statistical analyses of the data were carried out using Student's *t*-tests and analysis of variance (ANOVA).

## Results

### Apparent water permeability in *Palaemon longirostris*

#### Acclimated animals

The apparent water permeability (AWP) of *Palaemon longirostris* was correlated directly with salinity and decreased (as indicated by a rise in the  $T_{1/2}$  of exchange) as the salinity of the external medium was lowered (Table 1). ANOVA showed that this salinity effect on AWP was significant ( $P < 0.001$ ).

#### Sudden salinity change

Prawns acclimated for 7 days to 0.5‰ and then transferred directly to 34‰ showed a significant rise ( $P < 0.001$ ) in AWP (reduction of  $T_{1/2}$ ) after salinity transfer compared with acclimated animals (Fig. 1). The AWP for prawns acclimated to 34‰ and transferred to 0.5‰, however, was not significantly different ( $P > 0.05$ ) from that of prawns acclimated to 34‰ for 7 days (Fig. 1). Interestingly, the  $T_{1/2}$  of exchange for prawns transferred from 34 to 0.5‰ was significantly lower ( $P < 0.001$ ) than the  $T_{1/2}$  of exchange for prawns acclimated for 7 days to 0.5‰, indicating that acclimation time plays an important role in the reduction of apparent permeability to water of *P. longirostris* at low salinities. In contrast, the  $T_{1/2}$  of exchange for prawns transferred directly from 0.5 to 34‰ was not significantly different from the  $T_{1/2}$  of exchange for prawns acclimated for

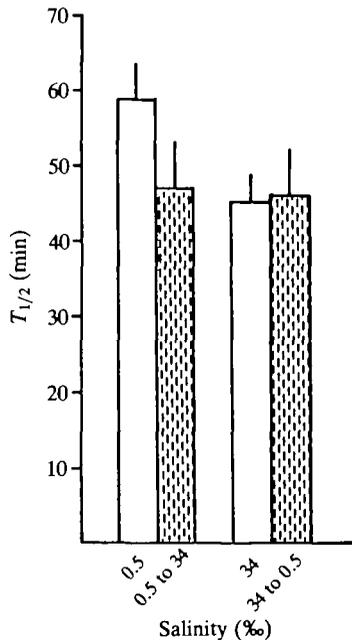


Fig. 1. Comparison of apparent permeability to water ( $T_{1/2}$ ) of *Palaemon longirostris* acclimated for 7 days at 0.5 or 34‰ (clear histograms) with that of individuals measured immediately after salinity transfer (shaded histograms) at 12°C. Mean  $\pm$  s.d. ( $N=10$ ).

Table 1. Comparison of the osmotic gradients, net water fluxes and permeability constants ( $T_{1/2}$ ) for four euryhaline prawn species in different salinities

	<i>Palaemon longirostris</i>		<i>Palaemonetes varians</i>		<i>Crangon crangon</i>		<i>Palaemon elegans</i>				
Salinity (‰)	0.5	7.0	22.0	34.0	34.0	43.0	7.0	22.0	34.0	34.0	
Osmotic gradient (mosmol kg <sup>-1</sup> )	+492	+423	+13	-395	-451	+378	+201	+16	-81	+75	-220
Net water flux (% body water day <sup>-1</sup> )	15.3 (43.7)	15.0	0.4	15.7	21.7	14.8 (18.0)	13.9	4.3	2.95	1.8 (2.4)	14.1
$T_{1/2}$ (min)	58.7	53.3	46.7	45.3	37.7	47.4	43.7	38.0	34.4	32.5	28.9
Data source	Campbell and Jones (1989a)			Hagerman and Uglow (1983)		Spaargaren (1971)	Ramirez de Isla		Hernandez and Taylor (1985)		
Temperature (°C)		12		12		12 and 15					

Osmotic gradient and mole fraction data used to calculate net water fluxes were obtained from the literature cited.

Figures in parentheses represent urinary flow rates (at 18°C) measured by direct cannulation of the excretory pore by Parry (1955) and converted to % body water day<sup>-1</sup>.

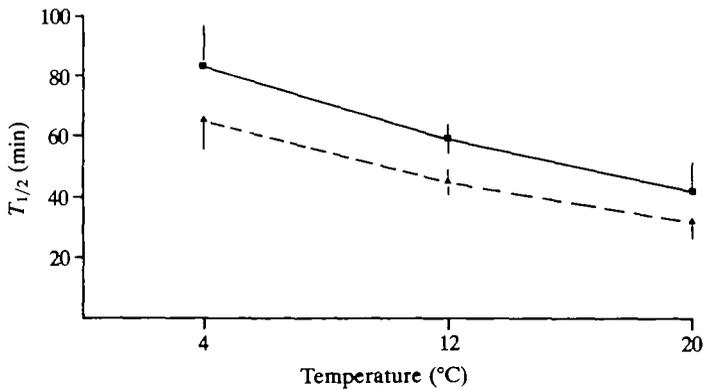


Fig. 2. Effect of temperature on the apparent permeability to water ( $T_{1/2}$ ) of *Palaemon longirostris* acclimated to 0.5‰ (■) or 34‰ (▲). Mean  $\pm$  s.d. ( $N=10$ ).

7 days to 34‰ ( $P>0.05$ ). Thus, acclimation time appears not to affect the AWP in *P. longirostris* at high salinities.

#### Temperature effects on apparent permeability to water

Values of  $T_{1/2}$  for *Palaemon longirostris* acclimated to 0.5 and 34‰ at each experimental temperature are shown in Fig. 2. A decrease in temperature resulted in a significant drop in AWP at each salinity ( $P<0.001$ ). The relative magnitudes of the temperature-related changes in AWP were compared by calculating the  $Q_{10}$  values at each salinity. The  $Q_{10}$  values were almost identical at 0.5‰ (1.54) and 34‰ (1.56).

#### Net osmotic flow in whole organisms

The net osmotic fluxes were calculated from the  $T_{1/2}$  of exchange and the osmotic concentrations of the haemolymph and the external medium. Net water movements (expressed as a percentage of body water exchanged per minute) were calculated from the following equation (Lockwood and Inman, 1973):

$$F = 100(\ln 2/T_{1/2}), \quad (1)$$

where  $F$  is the water flux. Net osmotic water flow ( $Os$ ) was determined from the water flux data and was based on the difference in the mole fraction of water in the medium and haemolymph of the animal:

$$Os = (M_m - M_a/M_m)F, \quad (2)$$

where  $M_m$  is the mole fraction of water in the external medium and  $M_a$  is the mole fraction of water in the haemolymph. The mole fraction of the blood and the external medium is  $55.56/(55.56+L)$ , where  $L$  is the osmolal concentration of the medium or haemolymph between 0 and 1.

The calculated net fluxes for *Palaemon longirostris*, *Palaemonetes varians*, *Crangon crangon* and *Palaemon elegans* over a range of salinities at 12°C are

shown in Table 1. *Palaemon longirostris* maintained a net water flux of approximately 15 % body water day<sup>-1</sup> when acclimated to salinities of 0.5, 7 and 34 ‰; when prawns were isosmotic with the external medium (22 ‰), net water fluxes were reduced to almost zero. The other prawns showed similar values of net water fluxes, although *C. crangon* had a relatively low exchange in 34 ‰ (Table 1).

#### Heart rate in *Palaemon longirostris*

To investigate whether the changes in AWP of *Palaemon longirostris* at low salinities were real body surface permeability changes or water flux variations caused by changes in the surface area over which water movement occurred (i.e. circulatory variations caused by changes in heart rate), the heart rate was measured in prawns acclimated to 0.5 and 34 ‰ at 4, 12 and 20 °C (Fig. 3). At each temperature, there was no significant change in heart rate between prawns in the two salinities ( $P > 0.05$ ).

#### Apparent water permeability in estuarine prawns

*Palaemonetes varians* showed a significant reduction of AWP (increase in  $T_{1/2}$ ) at 0.5 compared with 34 ‰ ( $P < 0.05$ ) (Fig. 4). The AWP of *Crangon crangon* also showed a significant reduction at low salinities ( $P < 0.01$ ). For *Palaemon elegans*, there was no significant change in AWP between the two salinities used (34 and 22 ‰) (Fig. 4); however, there was no major change in AWP for any prawn species between these two salinities.

Comparison of the AWP of *Palaemon longirostris* with those of the other prawn species revealed interesting differences (Fig. 4). At 0.5 ‰, *P. longirostris* showed a

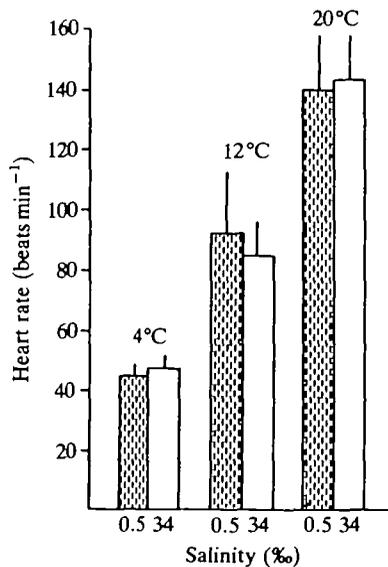


Fig. 3. Effect of salinity and temperature on the heart rate of *Palaemon longirostris* at 0.5 and 34 ‰. Mean  $\pm$  s.d. ( $N=5$ ).

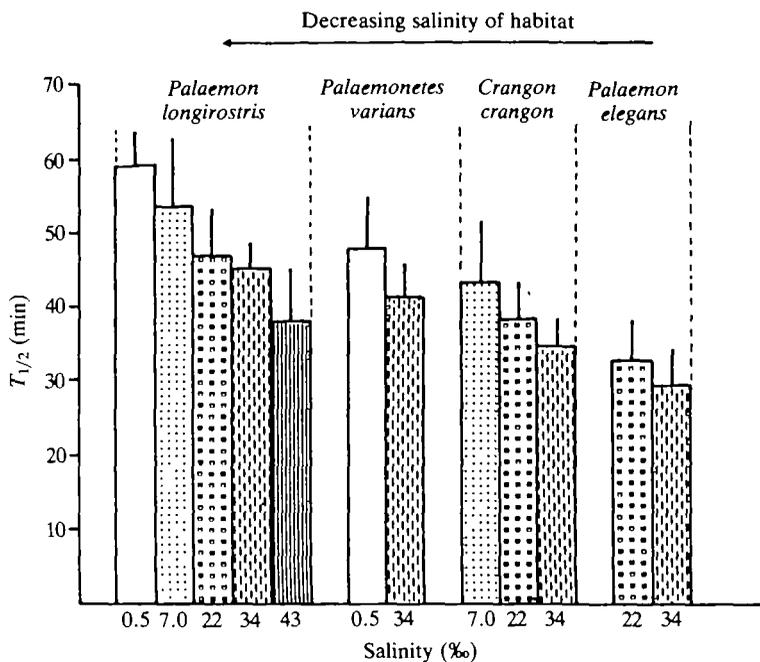


Fig. 4. Apparent permeability to water ( $T_{1/2}$ ) in relation to habitat salinity of *Palaemon longirostris*, *Palaemonetes varians*, *Crangon crangon* and *Palaemon elegans* exposed to different salinities at 12°C. Mean  $\pm$  S.D. ( $N=10$ ).

significantly lower AWP than *P. varians* ( $P<0.001$ ). Similarly at 7‰, *P. longirostris* has a significantly lower AWP than *C. crangon* ( $P<0.05$ ). At 22‰, the AWP's were in the order *P. longirostris*<*C. crangon*<*P. elegans* ( $P<0.001$ ). At 34‰, the AWP's were in the order *P. longirostris*<*P. varians*<*C. crangon*<*P. elegans* ( $P<0.001$ ). Thus, at each salinity, *Palaemon longirostris* had the lowest AWP, *Palaemonetes varians* had a lower AWP than *Crangon crangon*, and *Palaemon elegans* had the highest AWP.

### Discussion

Of the prawn species studied here, *Palaemon longirostris*, *Crangon crangon* and *Palaemonetes varians* were able to reduce their AWP's when acclimated to dilute sea water. Shaner *et al.* (1985) reported a similar reduction in AWP at low salinity (5‰ sea water) for the estuarine prawn *Crangon franciscorum*. The findings for *P. varians*, however, contradict earlier work, as both Parry (1955) and Rudy (1967) reported that this species did not alter its AWP as the concentration of the external medium was changed. This apparent anomaly may be explained by differences related to acclimatization of geographically separated populations to the salinity conditions of their specific habitat (Shaner *et al.* 1985). *P. varians* used in this study occupied regions characterized by extreme fluctuations in salinity (i.e.

conditions varying from fresh water to marine, depending on the state of the tide), whereas the study populations used by Rudy (1967) and Parry (1955) may have occupied regions characterized by smaller tidal variations in salinity. The results of this study, and those of Shaner *et al.* (1985), strongly suggest that a reduction of AWP at low salinity is a response that may be typical of estuarine and brackish-water prawns. This is not surprising, as such prawns often experience considerable periods in dilute saline waters. Animals living under dilute saline conditions gain water primarily by osmotic uptake. Expulsion of this water takes place mainly in the form of urine production, which also involves ion loss to the environment. Reduction of the AWP decreases osmotic entry of water, which in turn reduces urine production and ion loss to the environment (Kirschner, 1979). Reduction of AWP is regarded as a significant physiological adaptation to life in low-salinity environments, as it effectively reduces the energy required to maintain stable blood ionic concentrations by active ion uptake. It has also been postulated that maintenance of a comparatively high AWP at high salinities is also adaptive for such estuarine crustaceans, since maximization of water gain across the integument ensures sufficient urine for excretory purposes (Lockwood and Inman, 1973).

Cornell (1973) suggested that a drop in heart rate at low salinities may account for the associated drop in AWP of a species. For *Palaemon longirostris*, however, salinity had no significant effect on heart rate, and this is consistent with other studies with the freshwater prawn *Palaemon adspersus* (Hagerman and Uglow, 1979), the shore crab *Carcinus maenas* (Hume and Berlind, 1976) and the euryhaline amphipod *Gammarus duebeni* (Bolt *et al.* 1980). Thus, the salinity-induced changes in AWP of *P. longirostris* and other estuarine crustaceans appear to reflect real changes in integumental permeability.

The net water fluxes calculated for *P. longirostris* (15% body water day<sup>-1</sup>) were similar to those calculated for the other euryhaline prawns *Palaemonetes varians*, *Crangon crangon* and *Palaemon elegans* (Table 1). However, *P. longirostris* was able to maintain higher osmotic gradients between its blood and the external medium than the other species for a similar net water flux (Table 1). For example, when *P. longirostris* and *P. varians* were acclimated to 0.5‰, *P. longirostris* was able to maintain a net water flux almost identical to that of *P. varians*, even though the osmotic gradient between its blood and the external medium was 100 mosmol kg<sup>-1</sup> larger than that for *P. varians* (Table 1). Net water fluxes of comparable magnitude (20.5% body water day<sup>-1</sup>) have been reported for another estuarine prawn, *Crangon franciscorum* (Shaner *et al.* 1985). Thus, one very important adaptation possessed by estuarine prawns is an ability to maintain a relatively low net water flux, even when experiencing a large osmotic gradient between the blood and the external medium.

When prawns are hyperosmotic to the external medium, the calculated net water fluxes have been taken to represent a minimum estimate of urinary flow rates. Estimates of urine production in *Palaemonetes varians* and *Palaemon elegans* were comparable with those obtained for the same species by Parry (1955)

using direct cannulation of the excretory pore (Table 1). The urine flow rate obtained by Parry (1955) for *Palaemon longirostris* acclimated to 7‰ sea water, however, was three times larger than the urine flow rate predicted in this study (Table 1).

The finding that the AWP of *Palaemon longirostris* increased following transfer from 0.5 to 34‰, while the blood osmotic concentration remained almost unchanged (Campbell and Jones, 1989a), suggests that strong ionic regulation (Campbell and Jones, 1989b) may be more important than permeability to water in maintaining constant blood osmolalities at high salinities. Prawns acclimated to 34‰ and transferred to 0.5‰ showed no immediate change in AWP. Acclimation to 0.5‰ for 7 days, however, resulted in a lowering of the AWP. The estuarine amphipod *Corophium volutator* (Taylor, 1985) and the estuarine prawn *Crangon franciscorum* (Shaner *et al.* 1985) showed similar reductions in AWP following transfer to dilute salinity, but after 5–6 weeks for the amphipod and 7 days for the prawn. The unchanged AWP for *P. longirostris* after transfer from 34 to 0.5‰ was accompanied by an initial large drop in blood osmolality (Campbell and Jones, 1989a). The corresponding reduction in AWP that occurred during the next 7 days was also accompanied by a gradual rise in blood osmolality to a new steady state (Campbell and Jones, 1989a). Hence, ionic regulation alone is not responsible for the maintenance of a large osmotic gradient between the blood and the external medium in *P. longirostris* acclimated to very low salinities. A reduction in AWP thus seems to play an important role in the osmoregulation of *P. longirostris* at low salinities. Although these AWP changes occurred too slowly to be effective within a tidal cycle, they would be of considerable advantage to *Palaemon longirostris*, which lives predominantly in dilute saline regions of estuaries.

The effect of temperature on AWP has been little studied in crustaceans, and the limited data available suggest that AWP is lowered by a reduction in temperature (Smith and Rudy, 1972; Hannan and Evans, 1973; Tun, 1975). The magnitude of the temperature effect on permeability can be quantified by calculating the  $Q_{10}$ . Smith and Rudy (1972) reported  $Q_{10}$  values (between 10 and 20°C) of 1.51 and 1.63 for the estuarine crab *Hemigrapsus nudus* acclimated to 95‰ and 60‰ sea water, respectively. Results of this study reported a mean  $Q_{10}$  value of 1.55 for *Palaemon longirostris* acclimated to 34‰ and 1.53 for prawns acclimated to 0.5‰. Tun (1975) reported  $Q_{10}$  values (between 4 and 14°C) for *Palaemonetes varians* of 1.57 for prawns acclimated to 100‰ sea water and 1.60 for those acclimated to 2‰ sea water.  $Q_{10}$  values for *P. varians* over a higher temperature range (14–24°C) increased to 2.11 in prawns acclimated to 100‰ sea water and to 2.04 in prawns acclimated to 2‰ sea water (Tun, 1975). Over the same temperature range (between 14 and 24°C),  $Q_{10}$  values for the semi-terrestrial crab *Uca pugnator* were 2.10 for crabs acclimated to 100‰ sea water and 1.73 for crabs acclimated to 3‰ sea water (Hannan and Evans, 1973). Therefore, changes at high water temperature appear to have a more pronounced effect on AWP than changes at low water temperature.

The temperature-induced changes in AWP for *Palaemon longirostris* were

correlated with temperature-induced changes in heart rate. At low temperature, a drop in heart rate occurred which implied a reduction in the blood flow through the gills. Such a reduction in gill blood flow would effectively reduce the surface area to volume ratio available for water exchange across the gills and would explain the associated drop in AWP. Although these temperature-induced changes in AWP do not represent real hydraulic changes in cuticular permeability, the resulting effect is a drop in the permeability to water of the animal, which still has biological significance for the energetics of the animal (Lockwood *et al.* 1982).

In general, AWP varies among different groups of aquatic crustaceans and is correlated with habitat. Rudy (1967) showed that the marine swimming crab *Macropipus depurator* (acclimated to 100% sea water) was three times more permeable to water than the intertidal shore crab *Carcinus maenas*, and that *C. maenas* (when acclimated to 40% sea water) was three times more permeable to water than the freshwater crayfish *Astacus fluviatilis* (acclimated to fresh water). Similarly, Bolt (1983) showed that the extremely euryhaline amphipod *Gammarus duebeni*, which often occupies very dilute saline habitats, possessed a lower AWP than the intertidal amphipods *Chaetogammarus marinus* and *Gammarus locusta*. Reduction of the AWP of animals inhabiting less saline areas is a useful physiological adaptation, as it effectively reduces the osmotic work load on such animals. Present results show a clear relationship between habitat salinity and the relative AWP for the prawns *Palaemon longirostris*, *Palaemonetes varians*, *Crangon crangon* and *Palaemon elegans*. Hence, *Palaemon longirostris*, which lives in the most dilute saline regions of estuaries (almost fresh water), showed the lowest AWP at all salinities. *Palaemonetes varians*, which inhabits brackish-water pools indirectly connected to the sea, showed a higher AWP than *P. longirostris* but a lower AWP than *C. crangon*, which occupies the lower regions of estuaries. The most marine species, *Palaemon elegans*, which occurs typically in intertidal rock pools, showed the highest AWP at each salinity tested.

These observations suggest that permeability to water may be one of the determining factors separating species that possess overlapping salinity tolerance ranges. The data also support the theory that one of the major physiological adaptations to life in very dilute saline environments is reduction of water permeability (Lockwood, 1976; Greenaway, 1979; Vernberg and Vernberg, 1983).

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### References

- BOLT, S. R. L. (1983). Haemolymph concentration and apparent permeability in varying salinity conditions of *Gammarus duebeni*, *Chaetogammarus marinus* and *Gammarus locusta*. *J. exp. Biol.* **107**, 129–140.

- BOLT, S. R. L. (1989). Invertebrate permeability with whole organisms. In *Water Transport in Biological Membranes*, vol. 2, *From Cells to Multicellular Barrier Systems* (ed. G. Benga), pp. 233–245. Boca Raton, Florida: CRC Press Inc.
- BOLT, S. R. L., DAWSON, M. E., INMAN, C. B. E. AND LOCKWOOD, A. P. M. (1980). Variation of apparent permeability to water and sodium transport in *Gammarus duebeni* exposed to fluctuating salinities. *Comp. Biochem. Physiol.* **67B**, 465–473.
- BROEKEMA, M. M. (1941). Seasonal movements and the osmotic behaviour of the shrimp, *Crangon crangon* L. *Arch. Neer. Zool.* **6**, 1–100.
- CAMPBELL, P. J. AND JONES, M. B. (1989a). Osmoregulation of the estuarine prawn *Palaemon longirostris* (Caridea: Palaemonidae). *J. mar. biol. Ass. U.K.* **69**, 261–272.
- CAMPBELL, P. J. AND JONES, M. B. (1989b). Ionic regulation of the estuarine prawn *Palaemon longirostris* (Caridea: Palaemonidae). *Ophelia* **30**, 141–154.
- CAMPBELL, P. J. AND JONES, M. B. (1990). Adaptations of the prawn *Palaemon longirostris* (Crustacea, Decapoda) to life in dilute saline regions of estuaries: Effect of body size, temperature and season on salinity tolerance. *Proceedings of the 22nd European Marine Biological Symposium*, Barcelona, September 1987 (in press).
- CORNELL, J. C. (1973). A reduction in water permeability in response to a dilute medium in the stenohaline crab *Libinia emarginata* (Brachyura, Majidae). *Biol. Bull. mar. biol. Lab., Woods Hole* **145**, 430–431.
- CUMBRIDGE, N. AND UGLOW, R. F. (1977). Heart and scaphognathite activity in the shore crab *Carcinus maenas* (L.). *J. exp. mar. Biol. Ecol.* **28**, 87–107.
- DYER, M. F. AND UGLOW, R. F. (1977). On a technique for monitoring heart and scaphognathite activity in *Natantia*. *J. exp. mar. Biol. Ecol.* **27**, 117–124.
- GILLES, R. (1975). Mechanisms of ion and osmoregulation: Physiological Mechanisms. In *Marine Ecology*, vol. 2, part 1 (ed. O. Kinne), pp. 259–441. New York: Wiley-Interscience.
- GREENAWAY, P. (1979). Fresh water invertebrates. In *Comparative Physiology of Osmoregulation in Animals*, vol. 1 (ed. G. M. O. Maloij), pp. 117–173. London: Academic Press.
- HAGERMAN, L. AND UGLOW, R. F. (1979). Heart and scaphognathite activity in the shrimp *Palaemon adspersus* Rathke. *Ophelia* **18**, 89–96.
- HAGERMAN, L. AND UGLOW, R. F. (1983). The influence of temperature on the osmoregulation of the brackish-water shrimp *Palaemonetes varians* Leach. *Ophelia* **22**, 229–236.
- HANNAN, J. V. AND EVANS, D. H. (1973). Water permeability in some euryhaline decapods and *Limulus polyphemus*. *Comp. Biochem. Physiol.* **44A**, 1199–1213.
- HUME, R. I. AND BERLIND, A. (1976). Heart and scaphognathite rate changes in a euryhaline crab, *Carcinus maenas*, exposed to dilute environmental medium. *Biol. Bull. mar. biol. Lab., Woods Hole* **150**, 241–254.
- JOHNSON, I. T. (1985). Studies on some responses of *Carcinus maenas* (L.) and other brachyurans to hypoxia and aerial exposure. DPhil thesis, University of Hull.
- KIRSCHNER, L. B. (1979). Control mechanisms in crustaceans and fishes. In *Mechanisms of Osmoregulation in Animals*, part C, *Control of the Extracellular Fluid Osmolarity* (ed. R. Gilles), pp. 157–222. New York: Wiley-Interscience.
- LOCKWOOD, A. P. M. (1976). Physiological adaptation to life in estuaries. In *Adaptation to Environment. Essays on the Physiology of Marine Animals* (ed. R. C. Newell), pp. 315–392. London: Butterworths.
- LOCKWOOD, A. P. M., BOLT, S. R. L. AND DAWSON, M. E. (1982). Water exchange across crustacean gills. In *Gills* (ed. D. H. Houlihan, J. C. Rankin and T. J. Shuttleworth). *Society for Experimental Biology Seminar Series* **16**, pp. 129–147. Cambridge: Cambridge University Press.
- LOCKWOOD, A. P. M. AND INMAN, C. B. E. (1973). Water uptake and loss in relation to the salinity of the medium in the amphipod crustacean *Gammarus duebeni*. *J. exp. Biol.* **58**, 149–163.
- LOCKWOOD, A. P. M., INMAN, C. B. E. AND COURTNEY, T. H. (1973). The influence of environmental salinity on the water fluxes of the amphipod crustacean *Gammarus duebeni*. *J. exp. Biol.* **58**, 137–148.
- MANTEL, L. H. AND FARMER, L. L. (1983). Osmotic and ionic regulation. In *The Biology of*

- Crustacea*, vol. 5, *Internal Anatomy and Physiological Regulation* (ed. D. E. Bliss), pp. 53–161. New York: Academic Press.
- PARRY, G. (1955). Urine production by the antennal glands of *Palaemonetes varians* (Leach). *J. exp. Biol.* **32**, 408–422.
- POTTS, W. T. M. AND PARRY, G. (1964). *Osmotic and Ionic Regulation in Animals*. New York: Macmillan.
- RAMIREZ DE ISLA HERNANDEZ, S. AND TAYLOR, A. C. (1985). The effect of temperature on osmotic and ionic regulation in the prawn, *Palaemon elegans* (Rathke). *Ophelia* **24**, 1–15.
- ROBERTSON, J. D. (1949). Ionic regulation in some marine invertebrates. *J. exp. Biol.* **26**, 182–200.
- RUDY, P. P. (1967). Water permeability in selected decapod Crustacea. *Comp. Biochem. Physiol.* **22**, 581–589.
- SHANER, S. W., CROWE, J. H. AND KNIGHT, A. W. (1985). Long-term adaptation to low salinities in the euryhaline shrimp *Crangon fransiscorum* (Stimpson). *J. exp. Zool.* **235**, 315–323.
- SMALDON, G. (1979). *British Coastal Shrimps and Prawns. Synopses of the British Fauna (New Series)* (ed. D. M. Kermack and R. S. K. Barnes). London: Academic Press. 126pp.
- SMITH, R. I. (1967). Osmotic regulation and adaptive reduction of water-permeability in a brackish-water crab, *Rhithropanopeus harrisi* (Brachyura, Xanthidae). *Biol. Bull. mar. biol. Lab., Woods Hole* **133**, 643–658.
- SMITH, R. I. (1970). The apparent water-permeability of *Carcinus maenas* (Crustacea, Brachyura, Portunidae) as a function of salinity. *Biol. Bull. mar. biol. Lab., Woods Hole* **139**, 351–362.
- SMITH, R. I. AND RUDY, P. P. (1972). Water-exchange in the crab *Hemigrapsus nudus* measured by use of deuterium and tritium oxides as tracers. *Biol. Bull. mar. biol. Lab., Woods Hole* **143**, 234–246.
- SPAARGAREN, D. H. (1971). Aspects of the osmotic regulation in the shrimps *Crangon crangon* and *Crangon allmanni*. *Neth. J. Sea Res.* **5**, 275–335.
- SPAARGAREN, D. H. (1979). Marine and brackish water animals. In *Comparative Physiology of Osmoregulation in Animals*, vol. 1 (ed. G. M. O. Maloiy), pp. 117–173. London: Academic Press.
- TAYLOR, P. M. (1985). Water balance in the estuarine crustacean *Corophium volutator* (Pallas) (Amphipoda). *J. exp. mar. Biol. Ecol.* **88**, 21–29.
- TUN, M. T. (1975). The influence of environmental calcium and temperature on the water fluxes of *Palaemonetes varians* (Leach). MSc thesis. University of Southampton.
- VERNBERG, F. J. AND VERNBERG, W. B. (1983). Freshwater adaptations. In *The Biology of Crustacea*, vol. 8, *Environmental Adaptations* (ed. D. E. Bliss), pp. 335–363. New York: Academic Press.