SOME EFFECTS
OF SALINITY AND TEMPERATURE
ON THE OSMOTIC AND IONIC REGULATION OF
PRAUNUS FLEXUOSUS (CRUSTACEA, MYSIDACEA)
FROM ISEFJORD

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ABSTRACT

The salinity tolerance, osmotic regulation and ionic regulation of the mysid crustacean, *Praunus flexuosus*, collected at the Isefjord, Denmark, has been investigated over a range of salinities, and at temperatures from 5 to 20 °C for both winter and summer animals.

Survival at low salinities was enhanced when the animals were kept at low temperatures, and this enhancement was especially pronounced in animals collected in winter.

A clear pattern of hyper/hypo-osmotic regulation was found, but no effect of season or temperature on the osmotic concentration was observed. The blood concentration of Isefjord animals was significantly lower at any given salinity than that of previously studied animals from Loch Etive, Scotland. This reduction is considered to be due to long-term acclimation, and the findings are compared with other crustacea where studies have been made on distinct populations.

The blood concentrations of sodium, potassium, calcium, magnesium and chloride were determined at three salinities, and found when totalled to account for the osmotic concentrations.

INTRODUCTION

The mysid crustacean *Praunus flexuosus* (Müller) is a common inhabitant of the shallow sublittoral of European coastal and brackish waters (Tattersall & Tattersall 1951). In Danish waters it generally occurs in shoals with the mysid *Neomysis vulgaris* (Thompson), although typically less common than *Neomysis* (Muus 1967). In the Isefjord, Rasmussen (1973) reports numerous records of abundant *P. flexuosus* and emphasises their vital importance in the ecology of the area as consumers of both phyto- and zoo-plankton and suspended material, and as food for many animal species. The biology and breeding of *P. flexuosus* has been described by Blegvad (1922) for Nyborg Fjord, Denmark, and by Mauchline (1971) for Loch Etive, Scotland.

A salinity tolerance range of 2-33 ‰ for *P. flexuosus* from Loch Etive, Scotland, was demonstrated by McLusky & Heard (1971), who also described its osmoregulatory capacity. In experiments conducted at 5 °C, it was found to be a hyper/hypo-osmoregulatory species with the body tissues experiencing the range 15-31 ‰ over the above salinity range, with the isosmotic point at 27 ‰.

The present paper deals with the salinity tolerance, osmoregulation and ionic regulation in a *P. flexuosus* population from the Isefjord, Denmark. This population experiences a stable salinity regime within the range 18-20 ‰ (Rasmussen 1973) whilst the water temperature varies from 0-2 °C in winter, up to over 20 °C in summer. In view of this wide temperature variation I examined the effect of temperature acclimation on the salinity tolerance and osmoregulatory processes of *P. flexuosus*. Osmoregulation in *Praunus inermis* (Rathke), a closely related species, is also described.

MATERIALS AND METHODS

P. flexuosus were collected by wading with a push-net in the shallow water of the Isefjord at Hammeren and at Vellerup, which are localities 51 and 53b of Rasmussen (1973). They were transported to the Marine Laboratory at Helsingør where they were kept in constant temperature rooms. During the experimental period (March-August 1978) the salinity at Hammeren remained at 18.5-20 ‰, whilst the water temperature was 1 °C in March, 4 °C in April, 17 °C in May, 18-22 °C in June and 21 °C in July. For initial experiments 'winter' animals collected in March and April were kept at 5 °C prior to use, whilst for later experiments 'summer' animals collected in June and July were kept at 20 °C prior to use. *P. inermis* were collected in July at Hammeren.

Salinity tolerance was determined by placing individual animals in dishes with water of known salinity in the range 0-37 ‰. The dishes were covered to prevent evporation, and the animals were not fed. Unfed animals lived for over 300 h and deaths before this time were considered to be due to the effects of salinity. Tolerance was expressed as the ability for half of the population to remain alive after a known time interval and denoted as LT_{50} (Lethal Time 50 %) at a known salinity. Where any animals remained alive at 300 h the % survival was calculated. The osmotic concentration of the blood was determined by the melting-point method (Hørlyck 1973). Samples of blood were collected from the heart and dorsal artery by piercing the thoracic somites underneath the posterior part of the carapace with a fine glass capillary whilst the animal was under paraffin. Prior to sampling the animals were kept for 48 h in dishes of known salinity, and before collection of the sample they were gently dried with a paper tissue. The salinity tolerance and the osmotic concentration of the blood were determined for both winter and summer animals at 5 °C, and

for winter animals at 5 °C, and for winter animals at 15 °C and for summer animals at 20 °C, using both male and female animals, in the size range 14-20 mm length. To evaluate the ability of the animals to adapt its blood concentration to new salinities, animals were transferred abruptly from sea water (28 ‰) to diluted sea water (3.5 ‰), and animals were then removed for sampling at hourly intervals.

The ionic composition of the blood was determined for animals maintained at 5 °C at 27.5, 18 and 10 ‰. Samples of blood were collected as above except that the tissue-dried animal was not held under paraffin. By applying careful suction to the capillary 1 μl of blood could be obtained, although in the case of potassium only 0.5 μl was withdrawn to avoid any risk of cellular contamination.

For the determination of chloride content the blood sample was used directly in a Radiometer CMT 10 Chloride titrator. This apparatus relies on the accurate determination of sample volume which was checked by the use of standard solutions in the same capillary used for the blood sample.

Cation concentrations were determined with a Unicam SP 90 atomic absorption spectrophotometer. For sodium analysis the 1 μl blood sample of one animals was diluted with 3 ml of deionised water. For potassium analysis, for which the apparatus is less sensitive, the blood of 2 or 3 animals was pooled and diluted with 1 ml of deionised water. For calcium analysis, the blood of 2 or 3 animals together was diluted with 1 ml of 0.78 % EDTA solution, to reduce sodium interference. For magnesium analysis, the blood of one animal was diluted with 3 ml of 0.78 % EDTA. The results are expressed as m equiv l^{-1}, and the mean and standard deviation calculated for each ion at each salinity.

RESULTS

Salinity tolerance

Fig. 1 shows the results of the salinity tolerance experiments. 'Winter' animals at 5 °C were able to tolerate at least 3.5 to 37 ‰ for over 300 h. which was the limit that had been set for the LT_{50}. They died almost immediately in freshwater, and the LT_{50} in 1.2 ‰ was 87 h. 'Winter' animals at 15 °C were less able to withstand low salinities, having an LT_{50} of 32 h at 3.5 ‰, compared to over 300 h at 5 °C.

'Summer' animals at 5 °C and at 20 °C both showed a progressive reduction of LT_{50} in salinities below 6 ‰. At 5 °C the LT_{50} was over 300 h at 6 ‰, then
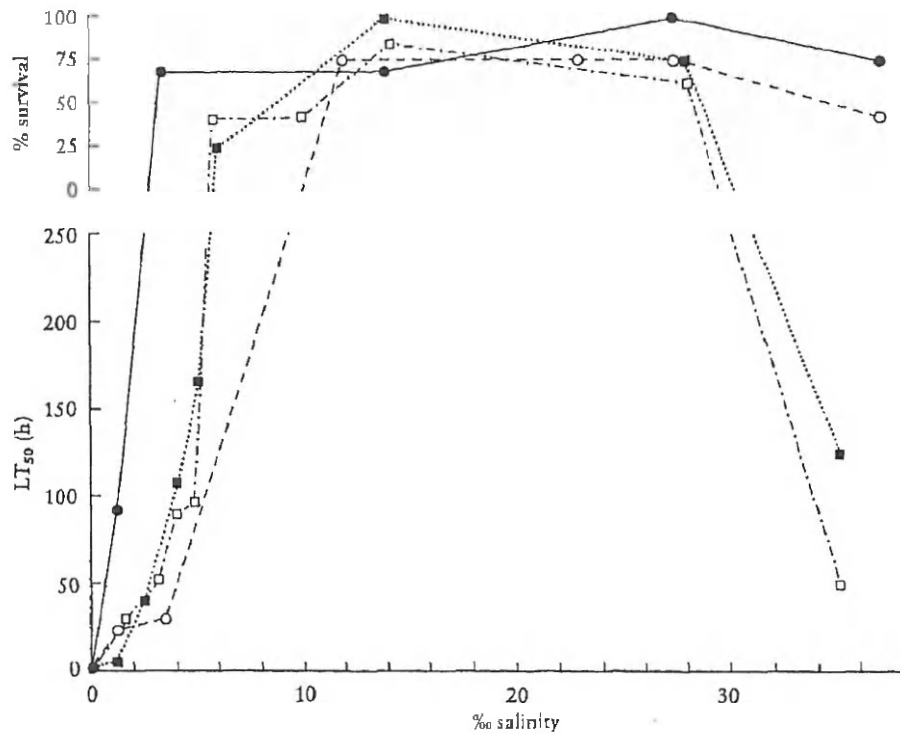
FIG. 1. The median lethal time (LT_{50}) of *Praunus flexuosus* in relation to salinity. For salinities where any animals remained alive at the end of 300 h the LT_{50} was deemed to be infinity, and the percentage survival at 300 h was calculated. Data are presented for winter animals at 5 °C (●) and 15 °C (○), and for summer animals at 5 °C (■) and 20 °C (□).

165 h at 5 ‰, 108 h at 4 ‰, 42 h at 2.5 ‰, and 4 h at 1.2 ‰. At 20 °C the comparable values for LT_{50} were 93 h at 5 ‰, 88 h at 4 ‰ and 53 h at 3 ‰. At 35 ‰ the LT_{50} was 126 h at 5 °C and 48 h at 20 °C.

The percentage-survival results reveal that the animals survived best at salinities between 12 and 30 ‰, with all treatments yielding 75 % or more survival at 300 h in these salinities. The results show an enhancement of survival at low salinities when the animals are kept at low temperature, which was especially pronounced in animals collected in winter.

Osmotic regulation

Figures 2 A-D show the osmotic concentration of the blood of *P. flexuosus*. All show a clear pattern of hyper/hypo-osmoregulation, with the blood concentration being maintained hypo-osmotic to the medium in salinities above 20–22 ‰, and hyper-osmotic to the medium in lower salinities. In winter animals

maintained at 5 °C (Fig. 2 A) this pattern of osmoregulation meant that over the range of salinities of 3 to 37‰, the blood concentration increased from 14‰ up to 27‰. The pattern of hyper/hypo-osmoregulation was extremely consistent in all experimental conditions. Thus in winter animals at 5 °C the isosmotic point was 21‰ and winter animals at 15 °C (Fig. 2B) had the isosmotic point almost identical at 22‰. Summer animals (Fig. 2 C & D) showed the same hyper/hypo-osmotic pattern with the isosmotic point at 21‰ at 5 °C, and at 20‰.
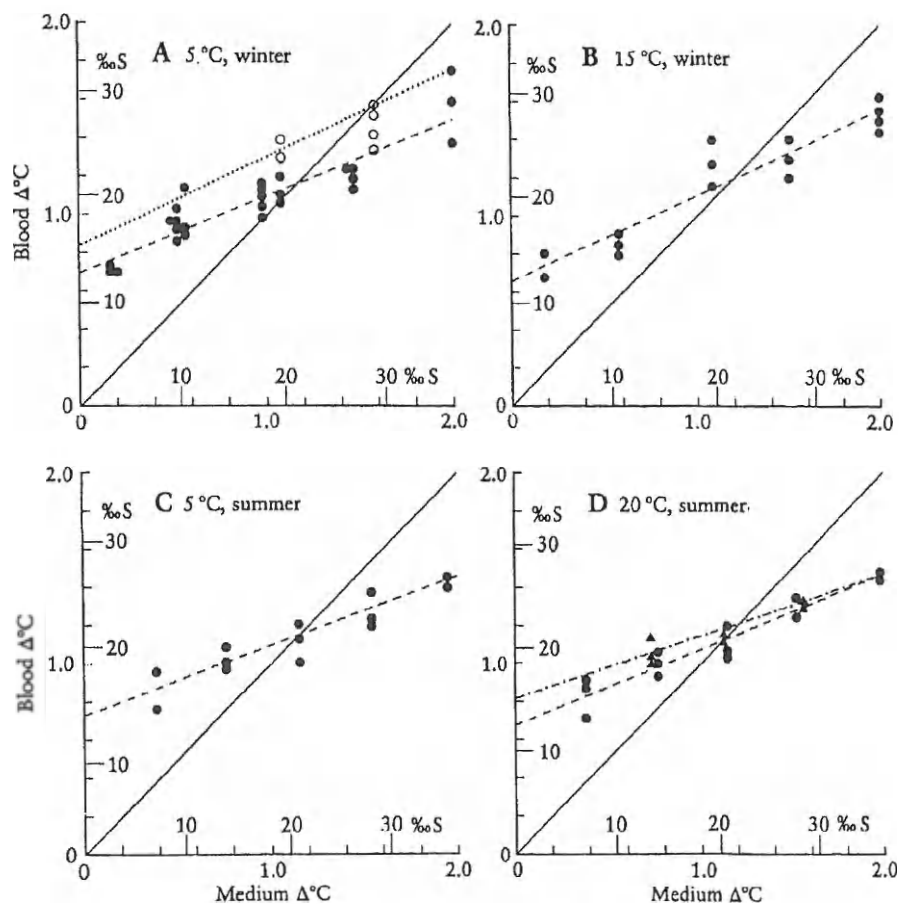

FIG. 2. The osmotic concentration of the blood of *Praunus flexuosus* in relation to salinity. The solid line indicates the isosmotic line, and the blood concentration of *P. flexuosus* from Isefjord is shown by the filled circles, with their regression shown by the dashed line. The open circles represent *P. flexuosus* from Nivå, and the dotted line represents the data of McLusky & Heard (1971) for *P. flexuosus* from Loch Etive. A, winter animals maintained at 5 °C. B, winter animals maintained at 15 °C. C, summer animals maintained at 5 °C. D, summer animals maintained at 20 °C. The blood concentration of *Praunus inermis* is shown by the triangles, and the dotted/dashed line.

TABLE 1. Blood concentration of *Praunus flexuosus* in relation to salinity. Where y = blood conc., x = medium, expressed as Δ °C

Experiment	Regression equation	Correlation coefficient	Number of observations
Winter 5 °C	y = 0.4045x + 0.6984	0.9209	26
Winter 15 °C	y = 0.4426x + 0.6625	0.9433	15
Summer 5 °C	y = 0.3462x + 0.7287	0.9281	13
Summer 20 °C	y = 0.3843x + 0.6857	0.9529	13
Loch Etive 5 °C (McLusky & Heard 1971)	y = 0.4461x + 0.8281	0.8637	54
P. inermis 20 °C	y = 0.3076x + 0.8194	0.9191	7

TABLE 2. Comparison of regression lines, presented in Table 1.

Comparison	Slope t	Slope Significance	Elevation t	Elevation Significance
Winter 5 °C v Winter 15 °C	0.6996	n.s.	0.1744	n.s.
Winter 5 °C v Summer 5 °C	0.9330	n.s.	0.9028	n.s.
Winter 5 °C v Summer 20 °C	0.2004	n.s.	0.9812	n.s.
Winter 15 °C v Summer 5 °C	1.3313	n.s.	0.9740	n.s.
Winter 15 °C v Summer 20 °C	0.7083	n.s.	0.8837	n.s.
Summer 5 °C v Summer 20 °C	0.6749	n.s.	0.1060	n.s.
Winter 5 °C v Loch Etive 5 °C	0.8279	n.s.	5.2200	P = <0.001
Winter 15 °C v Loch Etive 5 °C	0.0622	n.s.	4.3800	P = <0.001
Summer 5 °C v Loch Etive 5 °C	1.5842	n.s.	5.5300	P = <0.001
Summer 20 °C v Loch Etive 5 °C	0.7997	n.s.	5.5100	P = <0.001
P. flexuosus 20 °C v *P. inermis* 20 °C	1.1027	n.s.	1.8400	n.s.

Regression lines were calculated for each experimental treatment (Table 1), and in all cases the correlation coefficient of the regression was greater than 0.9 indicating a high degree of correlation. Statistical comparison of the regression lines revealed no significant differences in either slope or elevation (Table 2), and thus no significant effect of either season or temperature on the osmotic concentration of the blood of *P. flexuosus* from the Isefjord was found.

Tables 1 and 2 also include data from McLusky & Heard (1971) on the osmotic concentration of the blood of *P. flexuosus* from Loch Etive, Scotland. For these animals the isosmotic point was found to be at 27 ‰, and the slope of the regression of the Loch Etive data did not differ from the Isefjord results, but the elevation of the regression was significantly different (P = < 0.001) at all
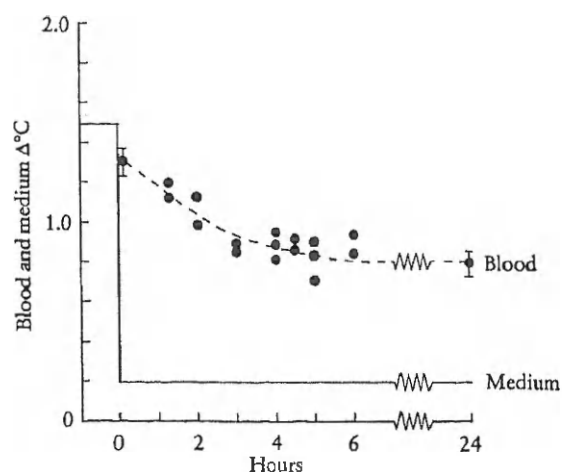
FIG. 3. The blood concentration of *Praunus flexuosus*, of animals transferred abruptly from sea water to dilute media (3.5 ‰ S), in relation to time after transferrance.

temperatures and seasons. Thus at any given salinity the Loch Etive animals had a higher blood concentration than the Isefjord animals. The blood concentration of a few *P. flexuosus* obtained from Nivå, 15 km south of Helsingør was similar to the Loch Etive animals (Fig. 2A).

When animals were transferred from sea water (28 ‰) into a diluted sea water (3.5 ‰) at 5 °C the blood concentration rapidly adjusted to the new conditions. Fig. 3 shows that over the first 3 h the blood concentration fell from 24 ‰ to 17 ‰ and down to 14.5 ‰, which was the new stable blood concentration, over the following 3 hours.

The blood concentration of *P. inermis* was determined for summer animals at 20 °C, and found not to differ significantly from *P. flexuosus* under the same conditions (Fig. 2D, Tables 1 & 2).

Ionic regulation

Table 3 shows the ionic composition of the haemolymph of *P. flexuosus*, with the mean and standard deviations for each ion at three salinities, as well as the ionic composition of the medium at each salinity. Sodium is maintained hypoionic to the medium in 27.5 ‰ sea water, and hyperionic in 18 and 10 ‰. Potassium and calcium are maintained hyperionic to the medium in all salinities, whilst magnesium is maintained markedly hypoionic in all salinities. Chloride is maintained hypoionic in 27.5 ‰, almost isoionic in 18 ‰ and hyperionic in 10 ‰.

TABLE 3. Ionic composition of the blood of *Praunus flexuosus*. All concentrations are expressed as m equiv l^{-1}.

Medium, ‰ Salinity	Ion	Blood, m equiv l^{-1} Mean	S.D.	Number of Observations	Medium, m eq l^{-1}
10	Sodium	243.0	41.0	6	137
18	–	261.8	21.4	6	246
27.5	–	294.7	47.9	7	376
10	Potassium	7.7	2.6	5	2.9
18	–	8.6	2.1	7	5.2
27.5	–	10.4	4.0	6	7.9
10	Magnesium	12.4	5.5	9	31.2
18	–	13.0	4.5	6	56.2
27.5	–	20.0	11.0	7	85.8
10	Calcium	10.1	1.7	7	5.9
18	–	11.8	1.9	5	10.7
27.5	–	20.8	3.5	10	16.4
10	Chloride	261.1	18.6	9	160
18	–	299.1	30.8	8	287
27.5	–	333.7	38.0	11	439

TABLE 4. Summation of the ionic composition of the blood of *P. flexuosus*.

Medium ‰ S.	f. pt.	Blood f. pt.	m eq l^{-1}*	Na$^+$	K$^+$	Mg^{2+}	Ca^{2+}	Total Cation	Cl$^-$	Total Anion**
10	0.55	0.95	278	243.0	7.7	12.4	10.1	273	261.1	289
18	0.98	1.10	322	261.8	8.6	13.0	11.8	295	299.7	328
27.5	1.49	1.19	348	294.7	10.4	20.0	20.8	346	333.7	362

* Freezing point may be converted to mmol NaCl equiv. 1^{-1} by the factor 293 (Nicol 1972)
** Including 28 m eq l^{-1} for SO$_4^{2+}$ (Nicol 1972).

A summation of the ionic concentrations is made in Table 4, and a comparison made with the results of the osmotic concentration. At 27.5 ‰ the total ionic concentration calculated from the osmotic concentration is 348 m eq 1^{-1}, whilst the sum of cations totals 346 m eq 1^{-1}, and the estimated anion total is 362 m eq 1^{-1}. At 18 ‰ the comparison is 322 m eq 1^{-1} from the osmotic concentration, 295 m eq 1^{-1} for cations and 328 m eq 1^{-1} for anions. At 10 ‰ the comparison is 278 m eq 1^{-1} from the osmotic concentration, 261 m eq 1^{-1} for cations and 289 m eq 1^{-1} for anions. Thus in general the ionic concentrations determined explain the osmotic concentration of the haemolymph.

DISCUSSION

The salinity tolerance experiments showed an absolute salinity tolerance range of at least 3.5 to 37 ‰ with maximal survival at salinities from 12 ‰ to 30 ‰, which may be compared to the environmental salinity of 18-20 ‰ in their Isefjord habitat. McLusky & Heard (1971) showed a similar salinity tolerance range of 2-33 ‰ for *P. flexuosus* from Loch Etive, maintained at 5 °C. Percival (1929) recorded *P. flexuosus* living in the Tamar estuary, England, at down to 0.3 ‰, which is certainly lower than the Isefjord population is able to withstand. Vlasblom & Elgershuizen (1977) found that *P. flexuosus* from Bommenee, Netherlands, collected at 28-30 ‰, showed highest survival between 14 and 36 ‰, and showed a marked decline in survival below 14 ‰. They also showed that the salinity tolerance of *P. flexuosus* was markedly affected by temperature, with only 10 % of the experimental population surviving 20 °C for 5 days. The environmental temperature at the time of their collection was 12.5-17 °C and it would appear that their population was less able to tolerate high temperatures than the Isefjord population which regularly experiences over 20 °C. For winter animals in the present study a clearly enhanced ability to withstand low salinities when combined with low temperatures has been shown. This is typical of temperate crustacea from low salinity regimes (Dorgelo 1976) and was also found by Vlasblom & Elgershuizen (1977).

A seasonal difference was apparent in the salinity tolerance results. In summer the beneficial effect of low temperature on tolerance of salinity extremes was less marked than in winter. Simmons & Knight (1975) found a significant effect of season on the respiration of the mysid, *Neomysis mercedis*, which they attributed to physiological changes preceding reproduction. In the present study the winter animals were predominately non-gravid females, whereas gravid females dominated the summer collections. Thus it may be that the different physiological state influenced the effects of salinity, with the gravid females being less able to withstand low salinities.

The clear pattern of hyper/hypo-osmoregulation in the blood *P. flexuosus* and *P. inermis* was also noted by McLusky & Heard (1971) for Scottish populations of the mysids *P. flexuosus* and *Neomysis integer* and by Dormaar & Corey (1973) for *Mysis stenolepis*, although Dormaar & Corey (1978) found that *Mysis relicta* was a hyper/iso-osmotic regulator. The hyper/hypo-osmoregulatory pattern is typical of many brackish-water crustacea (Kinne 1971; for review).

Weber & Spaargaren (1970) found an inverse correlation between temperature and blood concentration in *Crangon crangon*, whilst Dorgelo (1977) concluded that temperature had no effect on osmotic regulation in the populations of *Chaetogammarus marinus*, *Gammarus tigrinus* and *Gammarus fossarum* that he studied. In the present study no effect of either temperature (5, 15 or

20 °C) or seasonal acclimation (winter or summer) on the blood concentration of *P. flexuosus* has been found. This suggests that the Isefjord population is well adapted to cope with a wide range of environmental temperatures.

Comparison of the present results with those of McLusky & Heard (1971) reveals a statistically significant lowering of the blood concentration at all salinities in animals from Isefjord compared to those from Loch Etive. The animals in the Isefjord experience a stable salinity regime of 18.5-20 ‰, whereas those from Loch Etive experienced a fluctuating salinity regime of 2-18 ‰.

From these data one may ask why euryhaline crustacea from low salinity areas, when exposed to any given experimental salinity, maintain their blood concentration at a higher concentration than animals from high salinity areas exposed to the same experimental salinity? The present results suggests that the blood concentration of animals from different salinity regimes are normally adapted to be maintained at similar levels to each other, despite the differences in external salinity. For *P. flexuosus* from Isefjord at an external salinity of 18-20 ‰ the blood concentration is maintained at 19.8-21.3 ‰, whereas those from Loch Etive at an external salinity of 2-18 ‰ maintain their blood at 16.5-22.9 ‰. It is clear that despite the different environmental salinities the blood concentrations overlap considerably.

In *Mesidotea entonom* and *Gammarus duebeni*, Lockwood *et al.* (1976) showed that the blood concentration of fresh-water populations are maintained at levels similar to those maintained by brackish-water stocks. Similarly, Theede (1969) found that in low salinity the blood of *Carcinus* was of a higher osmotic concentration in animals from less saline areas. For *Crangon*, comparison of the results of Hagerman (1971) and Weber & Spaargaren (1970) shows that the blood concentration of animals from the Øresund (10-20 ‰) is maintained at a similar concentration (22-24.7 ‰) to that of animals from the Wadden Sea at Den Helder (26-33 ‰) which maintain their blood at 24.7-29.3 ‰.

The inverse relationship between environmental salinity and blood concentration shown here may thus be viewed as an enhancement of the hyper/hypo-osmotic regulation. For *P. flexuosus* the process of hyper/hypo-osmoregulation, with the level of regulation adjusted according to the normal external salinity, serves to keep the internal environment at 20 ± 3 ‰ in animals in their normal habitat.

The importance of environmental salinity in developing osmotic acclimation is shown by the limited results from Nivå. The salinity here is normally 8-10 ‰ (Muus 1967) and the animals showed a pattern of osmotic regulation more similar to that of the low salinity Loch Etive animals than the near-neighbouring but higher-salinity Isefjord animals. The small number of animals sampled from Nivå however makes statistical comparison invalid.

P. flexuosus is able to adapt quickly to (3-6 h) to a marked reduction in salinity. In this respect they closely resemble the euryhaline *Mysis stenolepis*,

which Dormaar & Corey (1973) found could adapt to all salinities other than 0 ‰ within 3 h. Together *P. flexuosus* and *M. stenolepis* provide a marked contrast to *Mysis relicta* which Dormaar & Corey (1978) found needed 5-6 days to adapt to new salinities.

The finding that *Praunus inermis* is a hyper/hypo-osmoregulator differs from the results of Belyaev (1949), who found that it was able to maintain the osmolarity af the body fluids constant over the range of salinity of 5-32 ‰, whereas the animals studied here show an increase of blood concentration from 16.5 to 25.1 ‰ over the same range.

To facilitate comparison between different species, Robertson (1949, 1953) expressed ionic concentrations as relative units, where chloride is expressed as 100 and the weights of other ions calculated on the basis of their atomic weight. In Table 5 the relative ionic composition of the blood of *P. flexuosus* at the three experimental salinities is presented, along with the data of Lucu (1978) for the mysid *Leptomysis mediterranea*, the data of Robertson (1949, 1953) for 15 marine crustacean species, and calculated data for 6 brackish-water crustacea maintained over the range 1-55 ‰ (*Corophium*, McLusky (1968); *Crangon*, Hagerman (1973); *Callinectes*, Engel (1977); *Hemigrapsus*, Dehnel (1967); *Leander* (*Palaemon*), Parry (1954); *Penaeus*, Venkataramiah *et al.* (1974)).

Comparison of the ionic composition of the blood of *P. flexuosus* with that of sea water reveals that at all 3 salinities studied the sodium content is kept proportionally a little higher than the chloride content. The potassium content is kept 60 % higher than sea water, the magnesium content is maintained at 25 ‰ of the level in sea water, and the calcium content is maintained approximately 30 % higher than sea water. Comparison with other species shows

TABLE 5. Relative ionic composition of the blood of marine and brackish Crustacea.

Ion Atomic weight	Cl^- 35.4	Na^+ 23.0	K^+ 39.1	Mg^{2+} 24.5	Ca^{2+} 40.1
P. flexuosus 10 ‰ (this paper)	100	60.4	3.25	3.28	4.38
P.flexuosus 18 ‰ —	100	56.7	3.17	3.01	4.47
P. flexuosus 27.5 ‰ —	100	57.4	3.45	4.15	7.07
Leptomysis 24.7 ‰ (Lucu 1978)	100	56.6	2.47	—	—
Leptomysis 36 ‰ —	100	55.5	2.68	—	—
Leptomysis 42.5 ‰ —	100	61.2	3.83	—	—
Brackish-water Crustacea 1-55 ‰, 6 spp.*	100	62.2	3.01	4.37	6.98
Marine Crustacea 15 spp. (Robertson 1949, 1953)	100	61.0	2.50	7.26	5.66
Sea water (Nicol 1972)	100	55.7	2.00	13.50	4.22

* Data from, and calculated from, McLusky (1968), Hagerman (1973), Parry (1954), Engel (1977), Dehnel (1967) and Venkataramiah *et al.* (1974).

All data calculated on a m equiv l^{-1} basis.

similar values for sodium in the mysid *Leptomysis mediterranea* and other marine and brackish-water crustacea. The potassium level in *P. flexuosus* is similar to that of *Leptomysis*, and the mean of the mysid values (3.14) is similar to other brackish-water crustacea, and slightly higher than the marine crustacea. Potassium values are notoriously liable to elevation if the blood is contaminated by any cellular material, and the differences noted should be viewed with caution. Robertson (1953) showed a range of magnesium values from 20 % of sea water in active crustacea to 100 % in less active species. The magnesium values for *P. flexuosus* (3.01-4.15) are 22-30 % of sea water and thus *P. flexuosus* is clearly among the more active species. Calcium values are liable to marked variation due to the moult cycle (Hagerman 1973), however it may be seen that the values for *P. flexuosus* are within the range noted for other marine and brackish-water crustacea, all being greater than sea water. The ionic concentrations determined account for the observed osmotic concentration of the blood, and together they show how well this population from the Isefjord is adapted to its habitat.

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