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EFFECT OF SALINITY ACCLIMATION ON OSMOREGULATION IN *CRANGON CRANGON* AND *PRAUNUS FLEXUOSUS*

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ABSTRACT

The effect of acclimation to low or high salinity on the osmoregulatory abilities of *Crangon crangon* L. (Crustacea, Natantia) from two habitats (Aberdour, Scotland and Øresund, Denmark) and *Praunus flexuosus* (Müller) (Crustacea, Mysidacea) from Øresund, Denmark has been investigated. The effect of salinity acclimation on the salinity tolerance of *Crangon* was also examined.

Animals acclimated for a long time to low salinity in the laboratory, or from low salinity habitats, were found to have enhanced hyperosmotic regulation when exposed to low salinities. Animals acclimated for a long time to high salinity in the laboratory, or from a high salinity habitat, were found to have enhanced hypo-osmotic regulation when exposed to high salinities. Acclimation to low salinity also extended the survival time in low salinities, and high salinity acclimation extended the survival time in high salinities.

It is shown that the difference in the osmoregulatory abilities of populations from different habitats are a phenotypic acclimation response and not a genetic difference between the populations, since if populations of *Crangon* or *Praunus* from different salinities are exposed to each other's salinity, they behave in the same manner as the population which is resident in that salinity.

INTRODUCTION

Studies of osmoregulation in crustacea have revealed various patterns of hyper-, hypo-, and iso-osmotic regulation (Kinne 1964, 1971; Lockwood 1977, for reviews). Almost all studies have however been conducted with single populations of the species involved from a single locality. Examination of the results of studies where populations from distinct habitats have been utilised shows distinct differences in osmoregulatory abilities between the populations.

Comparison of the results of Hagerman (1971) and Weber & Spaargaren (1970) shows that the blood concentration of *Crangon* from the Øresund (10-20 ‰) is maintained at a higher concentration in any given salinity than the blood of *Crangon* from the Wadden Sea (26-33 ‰). McLusky (1979) showed that *Praunus flexuosus* from Loch Etive, Scotland (2-18 ‰) maintain their blood

osmotic concentration at significantly higher levels in any given salinity than animals from Isefjord, Denmark (18-20 ‰). Lockwood *et al.* (1976) showed that the blood concentrations of fresh-water populations of *Gammarus duebeni* and *Mesidotea entomon* are maintained at similar levels to those maintained by brackish-water stocks. In each case where the osmoregulatory capabilities of different populations of crustacea are known, it is clear that animals from the lower salinity habitat maintain a greater osmotic difference to any given salinity than animals from a higher salinity habitat. McLusky (1979) suggested that this effect may serve to maintain the blood concentration of animals from different salinity regimes at similar levels to each other despite the differences in the salinity of the natural habitat.

Theede (1969) compared osmoregulation in *Carcinus maenas* from Kiel Bay in the Baltic Sea (13-18 ‰) with animals from Helgoland in the North Sea (32 ‰) and found that the blood of crabs from the Baltic Sea had a greater osmotic concentration and higher sodium concentration than the blood of animals from the North Sea when each were kept at 5-10 ‰. Exchanging animals caused the differences between the populations to be reduced, but not completely eradicated after 2-3 weeks. To our knowledge no other work has been conducted to see whether the observed differences in osmoregulatory ability between populations of crustacea from different salinity habitats are persistent (i.e. genetic) or are the result of long-term non-genetic acclimation. Indeed, Kinne (1971) commented that although the effect of temperature acclimation on osmoregulation was well studied, little was known on the effects of salinity acclimation on osmoregulation.

The present paper describes experiments on the effect of salinity acclimation on the osmoregulatory abilities of *Crangon crangon* and *Praunus flexuosus*. We aim to examine whether the previously oberved differences in the osmoregulatory performance of populations of *Crangon* and *Praunus* are the result of genetic isolation, or are an acclimation response to the salinities of different habitats.

This study was conducted at the University of Stirling and at the Marine Biological Laboratory, Helsingør. The first author is grateful for assistance from the Royal Society (Browne Research Fund). Statistical help was provided by W. Nicolaisen.

MATERIALS AND METHODS

For the first series of experiments, *Crangon crangon* L. (= *C. vulgaris* (Fabr.)) (Crustacea: Natantia) were collected at Silversands Bay, Aberdour, Scotland. During the period of collection (July-September 1979) the salinity was in the range 29.8-32.5 ‰, and the temperature between 10 and 15 °C. In the laboratory, animals were placed in aerated aquaria at either 6.9 ‰ or 40 ‰, and kept at 12 (±1) °C for 6 weeks. The animals were fed regularly and any dead animals

removed. The salinity of the aquaria water was checked at weekly intervals. At the end of the 6 week acclimation period animals were transferred to salinities of 6.9, 10, 15, 20, 25, 30, 40‰. After 24 hours in these salinities, blood samples were taken as described by Hagerman (1971), and the melting point determined in apparatus as described by Coast (1973). Only animals in the intermoult stages C-D were used for blood sampling. Animals between pro-ecdysis (stage D_3) and postecdysis (stage B) were not used as Hagerman (1973) has shown vast changes in ionic level of the haemolymph during moulting in this species.

For the second series of experiments with *Crangon*, animals were collected at Julebæk, Øresund, Denmark. During the period of collection (May-July 1981) the salinity was in the range 10-13‰, and the temperature at 10-16°C. In the laboratory, animals were placed in aquaria at 35‰ or 7‰, at 10(±1)°C for 3-6 weeks. At the end of the acclimation period animals were transferred to salinities of 5, 10, 15, 20, 25, 30, 35, and 40‰ for 24 hours. Blood samples were then taken and the osmotic concentration of the blood determined by the melting-point method (Hørlyck 1973).

Praunus flexuosus (Müller) (Crustacea: Natantia) were collected from Nordhavn, Helsingør, Denmark. During the period of collection (May-June 1981) the salinity was in the range 10-13‰, and the temperature was 10-16°C. In the laboratory, animals were placed in aerated aquaria at either 35 or 10‰, at 10(±1)°C for at least 3 weeks. At the end of this acclimation period, animals were transferred to salinities of 5, 10, 20, 30, and 35‰ for 24 hours. Blood samples were then collected, and the osmotic concentration determined as described by McLusky (1979).

Osmotic concentrations of the blood and the medium are expressed as the depression of the freezing point (Δ°C), which may be converted to salinity according to the relationship, $0.545\Delta°C = 10‰$ salinity. Both *Crangon* and *Praunus* are known to be able to adjust to a new salinity within 6 hours of transference to it (Hagerman 1971, McLusky 1979), so it is considered that the 24 hour period of adjustment to a new salinity used in the present study is an adequate time for the animals to adjust their blood concentration to that salinity.

The salinity tolerance of *Crangon* from Aberdour which had been acclimated for 6 weeks to low (6.9‰) and high (40‰) was determined by placing animals in dishes with water of 3.4, 6.9, 40 or 50‰ at 12°C. Unfed animals lived for over 240 hours 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 experimental population to remain alive after a known time interval and denoted as LT_{50} (Lethal Time 50%). Where any animals remained alive at 240 h the LT_{50} was recorded as 'over 240'.

RESULTS

The results of the first experiment with *Crangon* from Aberdour (30-33 ‰), show a distinct pattern of hyper/hypoosmoregulation (Fig. 1). This pattern can be conveniently divided into three portions. In salinities of 6.9-15 ‰ the blood is hyperosmotic, roughly paralleling the iso-osmotic line, thus the animals maintain a consistent difference between the blood and the medium over these salinities. In salinities of 20-25 ‰ the blood concentration is virtually independent of changes in the medium, and remains constant at about 24 ‰. In higher salinities (30-40 ‰) the blood is predominantly maintained hypo-osmotic to the medium, again paralleling the iso-osmotic line and thus maintaining a consistent difference between the blood and the medium over these salinities.

To aid in the analysis of the osmotic response to different salinities, regression equations were calculated for each of the three portions of the blood osmotic concentration curve. Table 1 shows the results for the three portions. Compari-

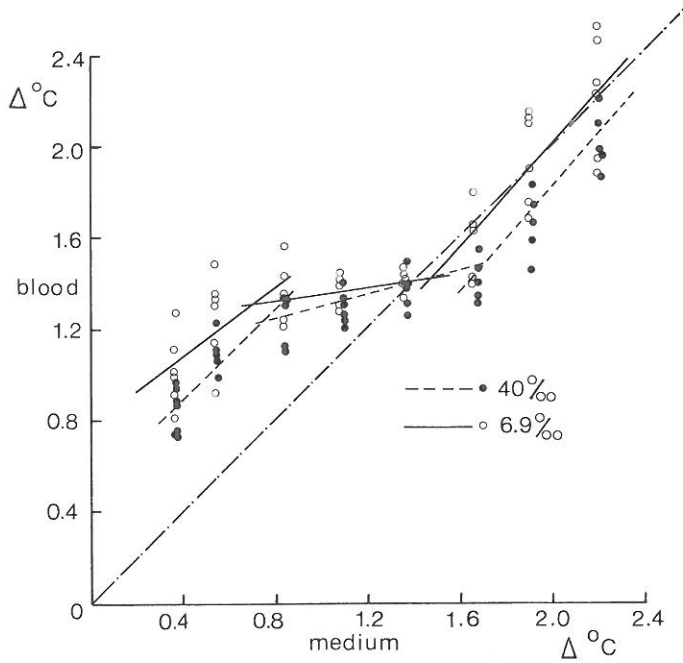

FIG. 1. The osmotic concentration of the blood of *Crangon crangon* in relation to salinity. These animals were collected at Aberdour, Scotland, where the salinity was 30-33 ‰, and then acclimated for 6 weeks to either 6.9 or 40 ‰ prior to sampling. The blood concentration of animals kept at 6.9 ‰ is shown by the open circles, and their regressions are shown by the solid lines. The blood concentrations of animals kept at 40 ‰ is shown by the filled circles, and their regressions are shown by the dashed lines. The isosmotic line is indicated as a dashed/dotted line.

TABLE 1. Blood concentration of *Crangon* and *Praunus* in relation to salinity. Where y = blood concentration, x = medium, expressed as Δ°C. Salinity expressed as ‰ NaCl.

Reference number	Animal	Habitat	Acclimation salinity (3-6 weeks)	Experimental salinity (24 h)	Regression equation	Correlation coefficient	Number of observations
1	*Crangon*	Aberdour	6.9	6.9-15	$y = 0.758x + 0.773$	0.632	17
2	–	(30-33 ‰)	40	6.9-15	$y = 0.942x + 0.512$	0.836	17
3	–	–	6.9	20-25	$y = 0.139x + 1.223$	0.307	10
4	–	–	40	20-25	$y = 0.250x + 1.031$	0.427	11
5	–	–	6.9	30-40	$y = 1.153x - 0.283$	0.782	17
6	–	–	40	30-40	$y = 1.143x - 0.482$	0.911	15
7	–	Øresund	7	5-15	$y = 0.335x + 0.914$	0.843	19
8	–	(10-13 ‰)	35	5-15	$y = 0.448x + 0.776$	0.780	16
9	–	–	7	20-25	$y = 0.071x + 1.196$	0.339	8
10	–	–	35	20-25	$y = 0.242x + 1.045$	0.522	8
11	–	–	7	30-40	$y = 0.894x + 0.107$	0.974	18
12	–	–	35	30-40	$y = 0.610x + 0.475$	0.926	17
13	*Praunus*	–	10	5-35	$y = 0.391x + 0.799$	0.940	20
14	–	–	35	5-35	$y = 0.372x + 0.739$	0.956	29

son of these regression equations (Table 2) reveals that for the Aberdour animals there is a significant difference in the elevation of the regression line for the blood of animals acclimated to 6.9 and 40 ‰ when exposed to 6.9-15 or 30-40 ‰, but no difference in the blood concentration at 20-25 ‰. The result of a significant difference in elevation indicates that low salinity (6.9 ‰) acclimated animals maintain a greater degree of hyper-osmoticity when exposed to low

TABLE 2. Comparison of regression equations, presented in Table 1, comparing low and high salinity acclimation levels. Reference numbers as per Table 1.

Comparison	Slope		Elevation	
	t	Significance	t	Significance
Crangon 1 v 2	0.643	n.s.	3.063	P = <0.005
– 3 v 4	0.468	n.s.	1.802	n.s.
– 5 v 6	0.037	n.s.	3.469	P = <0.005
– 7 v 8	1.090	n.s.	4.169	P = <0.001
– 9 v 10	0.903	n.s.	1.607	n.s.
–11 v 12	3.482	P = <0.005	9.138	P = <0.001
Praunus 13 v 14	0.502	n.s.	3.430	P = <0.005

experimental salinities than do high salinity (40 ‰) acclimated animals. Furthermore, high salinity acclimated animals maintain a substantial degree of hypo-osmoticity when exposed to high experimental salinities, but low salinity acclimated animals are virtually iso-osmotic over the 30-40 ‰ salinity range.

Crangon collected from Øresund (10-13 ‰) showed a similar pattern of osmoregulation to that observed for the Aberdour animals, being hyperosmotic in low salinities and hypo-osmotic in high salinities (Fig. 2). The regression equations for the three portions (5-15, 20-25, 30-40 ‰) of the blood concentration curve, at the two acclimation salinities (7 and 35 ‰) are presented in Table 1. Comparison of these regression equations (Table 2) reveals that for the Øresund animals there is a significant elevation of the blood concentration, for low salinity (7 ‰) acclimated animals when placed in low experimental salinities (5-15 ‰), thus indicating an increased degree of hyper-osmoticity amongst these animals. No significant differences in slope or elevation of the regression lines was observed between animals exposed to 20-25 ‰. Animals exposed to 30-40 ‰ showed a significant difference in both slope and elevation between the two acclimation treatments. The regression lines, if extrapolated, meet at 1.30Δ°C (23.8 ‰), but over the experimental range of 30-40 ‰ show progressive divergence, with a significant difference in elevation, indicating that there is a significant effect of acclimation at 30 ‰ and that this effect increases towards

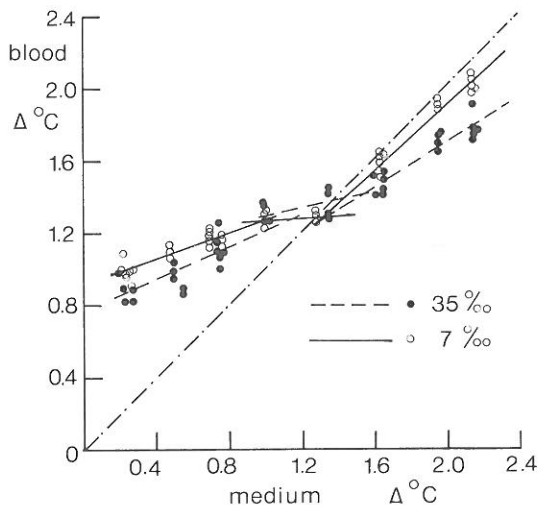

FIG. 2. The osmotic concentration of the blood of *Crangon crangon* in relation to salinity. These animals were collected at Øresund, Denmark, where the salinity was 10-13 ‰, and then acclimated for 3-6 weeks to either 7 or 35 ‰ prior to sampling. The blood concentration of animals kept at 7 ‰ is shown by the open circles, and their regressions are shown by the solid lines. The blood concentration of animals kept at 35 ‰ is shown by the filled circles, and their regressions are shown by the dashed lines. The isosmotic line is indicated as a dashed/dotted line.

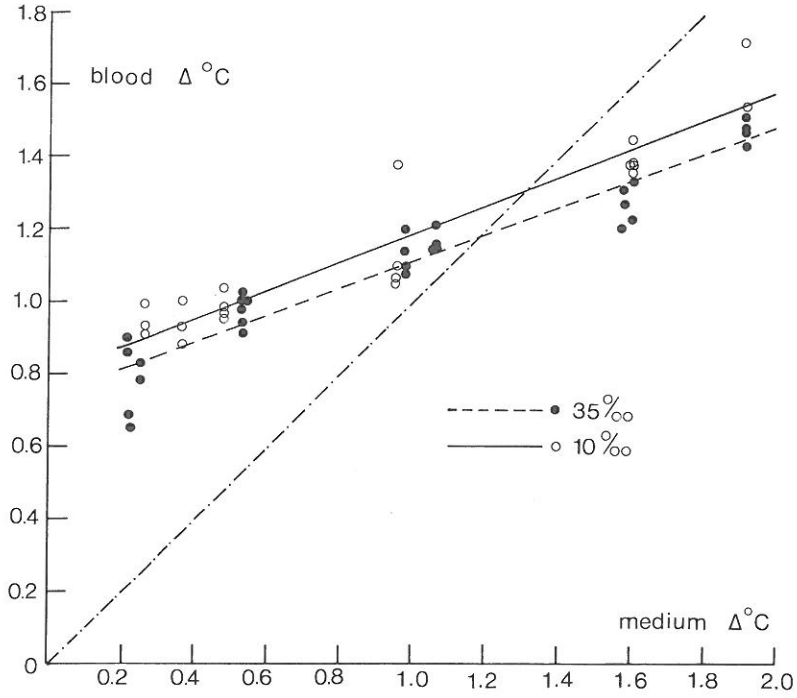

FIG. 3. The osmotic concentration of the blood of *Praunus flexuosus* in relation to salinity. These animals were collected at Øresund, Denmark, where the salinity was 10-13 ‰, and then acclimated for at least 3 weeks to either 10 or 35 ‰ prior to sampling. The blood concentration of animals kept at 10 ‰ is shown by the open circles, and their regression is shown by the solid line. The blood concentration of animals kept at 35 ‰ is shown by the filled circles, and their regression is shown by the dashed line. The isosmotic line is indicated as a dashed/dotted line.

40 ‰. This result indicates that high salinity acclimated animals maintain a greater degree of hypo-osmoticity than do low salinity acclimated animals.

Praunus collected from Øresund (10-13 ‰) show a clear pattern of hyper/hypo-osmotic regulation (Fig. 3). The pattern of osmotic regulation can be described by a single regression equation for each salinity acclimation experiment (Table 1). Comparison of the slope of the regression lines from each salinity acclimation indicates no significant difference, but the elevation of the slope is significantly different between animals acclimated at 10 ‰ and those acclimated at 35 ‰ (Table 2). This significant difference indicates that low salinity acclimated animals maintain a greater degree of hyper-osmoticity when exposed to low salinities, and a lesser degree of hypo-osmoticity than high salinity acclimated animals when exposed to high salinities. As a measure of the difference between the two acclimation conditions, the iso-osmotic point is 24 ‰ for low salinity acclimated animals, and 21.8 ‰ for high salinity acclimated animals.

TABLE 3. The median lethal time (LT_{50}) in hours of *Crangon crangon* acclimated to low (6.9 ‰) or high (40 ‰) salinities for 6 weeks, and then placed in salinities of 3.4-50 ‰. Where any animals remained alive at 240 h the LT_{50} is recorded as '>240 h'. Experiments conducted at 12 °C.

		Acclimation salinity (6 weeks)	
		6.9 ‰	40 ‰
Test salinity	3.4 ‰	>240	14
	6.9 ‰	>240	>240
	40 ‰	>240	>240
	50 ‰	16	38

The results of the salinity tolerance experiment showed that *Crangon* from both low and high salinity acclimation at 12 °C were able to tolerate 6.9 and 40 ‰ for over 240 h (Table 3). Animals from the low salinity acclimation showed enhanced survival at 3.4 ‰, being able to tolerate that salinity for over 240 h, whilst high salinity acclimated animals had an LT_{50} of 14 h at 3.4 ‰. High salinity acclimated animals were better able to cope with 50 ‰, having an LT_{50} of 38 h, whilst low salinity acclimated animals had an LT_{50} of 16 h at 50 ‰.

DISCUSSION

The present studies have shown hyper- and hypo-osmoregulation in *Crangon* and *Praunus* conforming to the overall patterns described for each species by Hagerman (1971) and McLusky (1979). The three present experiments with *Crangon* from Aberdour and Øresund and with *Praunus* from Øresund have all shown a clear effect of salinity acclimation as a factor modifying the established patterns of osmoregulation. In each study animals acclimated to low salinity regimes for periods of 3-6 weeks have maintained their blood significantly more hyperosmotic when exposed to low experimental salinities, and significantly less hypo-osmotic when exposed to high experimental salinities, than animals which had been acclimated for 3-6 weeks to high salinity regimes. In the case of *Crangon* no effect of acclimation was found in animals transferred to intermediate salinities (20-25 ‰), at which salinities the animals are near their isoosmotic point.

Previous studies of crustacea from different habitats have shown that animals from low salinity habitats maintain their blood concentration at a higher level than the blood of animals from high salinity habitats, when exposed to any given salinity (Theede 1969, Hagerman 1971, Weber & Spaargaren 1970,

McLusky 1979). The present experiments on animals acclimated in the laboratory for up to 6 weeks at high or low salinity clearly show a similar effect. A consistent pattern of results emerges such that animals from low salinity habitats or kept in the laboratory at low salinities show a significantly greater degree of hyper-osmoregulation when placed in low experimental salinities, than do animals from high salinity habitats or which had been kept in the laboratory at high salinities. These high salinity animals show a markedly greater degree of hypo-osmoregulation when placed in high experimental salinities.

Theede (1969) exchanged crabs from different salinity habitats, and found that the observed osmotic differences, although diminished, remained 2-3 weeks later. We have not been able to do direct exchange experiments, but the present studies do constitute the equivalence of exchange experiments between the populations of *Crangon* from the full-strength sea water of Aberdour and the reduced salinity environment of the Øresund, as each population has been acclimated in the laboratory to a salinity close to the other's natural habitat. This comparison (Table 4) shows that there is no significant difference between the two populations in the slope or elevation of the regression lines describing the osmotic concentration of the blood of animals exposed to similar levels of acclimation, or experimental salinities, except for two situations. For animals acclimated to low salinities and then exposed to 20-25 ‰ a difference in elevation can be noted. However, the regression lines describing these results have low correlation coefficients and the significance of the comparison is thereby reduced. In the case of high salinity acclimated animals exposed to 30-40 ‰, a significant difference in slope can be seen, but not of elevation, indicating that the regression lines cross each other.

Overall it may be stated that the two populations of *Crangon* from distinct habitats do show the same response to salinity changes as each other, and no

TABLE 4. Comparison of regression equations, presented in Table 1, comparing Aberdour and Øresund populations of *Crangon* exposed to similar experimental treatments. Reference numbers as per Table 1.

Comparison	Slope		Elevation	
	t	Significance	*t*	Significance
1 v 7	1.725	n.s.	2.240	n.s.
2 v 8	2.693	n.s.	0.523	n.s.
3 v 9	0.369	n.s.	4.043	P = <0.005
4 v 10	0.032	n.s.	0.125	n.s.
5 v 11	1.068	n.s.	1.999	n.s.
6 v 12	3.388	P = <0.005	1.646	n.s.

persistent differences such as those found by Theede (1969) were observed. Thus the differences in the osmotic performance of the populations can be considered as being entirely due to salinity acclimation rather than any genetic difference with the Aberdour animals naturally acclimated to 30-33 ‰, and the Øresund animals naturally acclimated to 10-13 ‰. If each population is acclimated to the other's salinity, it behaves in the same manner as the population which is resident in that salinity.

In the case of *Praunus* a difference in osmotic performance was noted between populations from different salinity habitats (Isefjord and Loch Etive) by McLusky (1979). The present studies indicate that this difference is due to salinity acclimation rather than any genetic difference between the populations, since a significant effect of acclimation comparable to the previously observed differences between the distinct populations can be produced after 3 weeks acclimation to a salinity regime in the laboratory.

Biggs & McDermott (1973) demonstrated that hermit crabs (*Pagurus longicarpus*) collected from environments in New Jersey with different mean salinities had different temperature and salinity tolerances, with those from high salinity environments able to tolerate higher salinities over a 96 h period, and animals from the low salinity environment able to tolerate lower salinities over the same time. They suggested that the observed differential tolerances may derive from osmotic considerations, but did not pursue the matter further. In a comparison of their osmoregulatory ability, Hørlyck (1973) showed that *Idotea viridis*, which is more tolerant of low salinity than *I. granulosa* or *I. baltica*, was also a significantly better osmoregulator than the other species. Anderson & Prosser (1953) noted that blue crabs (*Callinectes sapidus*) from low salinity environments were able to survive significantly longer in lower than 10 % sea water than crabs from high salinity environments, and further suggested that crabs from different minimal salinities differed in their state of osmotic adaptation. Tests which were not reported in detail had apparently indicated that these differences were phenotypic.

Kinne (1964) in a major review of the effects of salinity on salinity tolerance concluded that, in general, acclimation to low salinities tends to shift the lower lethal limit downward, and acclimation to higher salinities tends to shift the upper limit upwards. The present studies on the effect of salinity acclimation on salinity tolerance in *Crangon* show further confirmation of this view, with acclimation to 6.9 ‰ causing enhanced survival at 3.4 ‰, and acclimation to 40 ‰ causing enhanced survival at 50 ‰.

The results of the present study of osmoregulation may serve to provide an explanation for the observed effects of salinity acclimation on salinity tolerance. Our studies have shown that acclimation to low salinity, whether in the laboratory or in natural populations, causes a significant increase in the degree of hyperosmotic regulation in the blood of the crustacea examined, so that in any

given low salinity, the low salinity acclimated animals maintain a greater differential between the blood and the medium. We would suggest that this effect provides an enhancement of the normal hyperosmotic abilities of euryhaline crustacea in low salinities, and so enables low salinity acclimated animals to tolerate lower salinities still better. The increased hyperosmotic ability provides a higher degree of cell protection by surrounding the cells with a more stable body fluid. Conversely, high salinity acclimated animals, whether in the laboratory or in the field show a significant increase in the degree of hypo-osmotic regulation of their blood, so that in any given high salinity, they maintain a greater differential between the blood and the medium. This effect enhances the normal hypo-osmotic abilities of euryhaline crustacea in high salinities, and so enables high salinity acclimated animals to tolerate higher salinities, by again providing increased cell protection. We have also shown that the enhancement of osmotic regulation by salinity acclimation is a phenotypic response, at least in *Crangon* and *Praunus*, and is not due to any genetic difference between populations from different habitats.

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