

OSMOREGULATION IN THE *JAERA ALBIFRONS* GROUP OF SPECIES [ISOPODA, ASELLOTA]

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(Text-figs. 1-6)

An investigation into the osmoregulatory capabilities of *Jaera albifrons* Leach, *J. ischio-*
setosa Forsman, *J. praehirsuta* Forsman and *J. forsmanni* Bocquet has been carried out
comparing blood osmotic pressures of individual animals. Females only were used in the
experiments for three species owing to the extremely small size of the males, but some
large *J. forsmanni* males were successfully sampled for blood. The results correlate with the
known ecological distributions for each species, *J. ischio-*
setosa able to maintain a steady
internal osmotic pressure even in very dilute sea water and evidently the most capable
osmoregulator in the group. All four species regulate hyperosmotically in dilute sea
water, but *J. forsmanni* and *J. praehirsuta* appear to be less capable of maintaining a steady
state in almost fresh water, and appear to be the most marine members of the group. The
effects of temperature on the regulatory behaviour are discussed.

INTRODUCTION

The *Jaera albifrons* Leach group of species is a common component of estuarine faunas
in Britain, where each species may occur in considerable numbers. Some members of
the group also occur in less variable, marine localities in Britain and elsewhere, indicating
that each species is capable of survival in a wide range of salinity combinations and that
the group as a whole is euryhaline (see, for example, Naylor & Haahtela, 1966; Jones &
Naylor, 1971). Naylor & Haahtela (1966) showed that the four species of *Jaera* which
occur in Britain occupy preferred areas on an estuarine shore such that *Jaera ischio-*
setosa Forsman is common on stones in areas affected by freshwater seepage, *Jaera albifrons*
Leach occurs on stones either in pools or in parts of the shore where water is retained
(around M.T.L.), *Jaera praehirsuta* Forsman occurs on *Fucus serratus* (L.), and *Jaera*
forsmanni Bocquet can be found under stones around L.W.S.T.-L.W.N.T. where there is little
retention of water. A later investigation by Jones & Naylor (1971) has shown that these
habitat preferences persist throughout a 2-year period, and that each of the *Jaera* species
is capable of successful reproduction and development in a characteristic pattern of
fluctuation in salinity, temperature and exposure to air.

Kinne (1963, 1964, 1966) has summarized the effects of salinity and temperature on
estuarine animals, in some of which blood osmotic pressure conforms to salinity changes
while in others the internal osmotic pressure is regulated independently of the changes in
the outside medium (Prosser & Brown, 1961). Lockwood (1962) recognized two primary
types of osmoregulators - one which regulates hyposmotically in concentrated solutions
and hyperosmotically in dilute saline, and another which is isosmotic in high salinities

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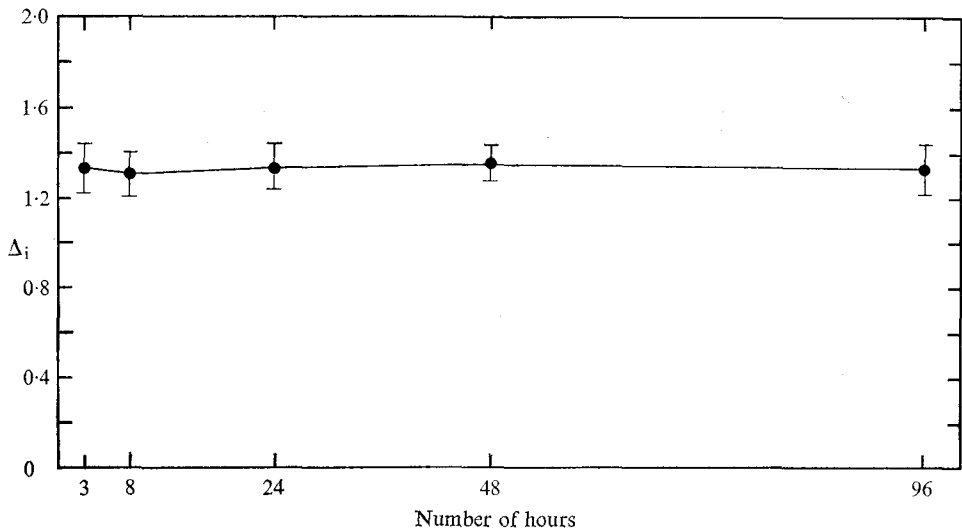


Fig. 1. The osmotic pressure of the blood of *Jaera albifrons* transferred directly from 100% s.w. at 17.5 °C to 5% s.w. at 17.5 °C plotted as mean Δ_i with standard deviations.

and hyperosmotic in dilute sea water. The occurrence of four very closely related species of *Jaera* in marine, estuarine and freshwater locations provides excellent material for a comparative physio-ecological study of osmoregulation in isopods – a subject which has been relatively little investigated. This investigation therefore set out to determine how each member of the *J. albifrons* group is able to live successfully in estuaries by examining blood osmotic pressures of individual animals exposed to different salinities, and to look for possible differences in these methods which could explain the individual ecological isolation which has undoubtedly led to their speciation.

MATERIALS AND METHODS

The members of the *J. albifrons* group can be identified only on the basis of the secondary sexual characters present on the male pereopods (Bocquet, 1950; Jones & Fordy, 1971; Naylor, 1972). The female pereopods are unmodified and are similar in each species. It was not possible to use the males of three *Jaera* species for this investigation due to their extremely small size, but the haemolymph of male and female *J. forsmanni* was successfully sampled. Females which are larger were used for the other three species, and these were collected from populations which a long-term study had shown to be 'pure' for the selected species (Jones & Naylor, 1971). Both gravid and non-reproductive females were used.

After collection animals were first acclimatized in water from the collection site at 8 °C and 17.5 ± 1 °C (for *J. forsmanni* at Plymouth the c.t. room was at 15 °C). After acclimatization to the temperature, for at least 24 h, animals were transferred to the experimental salinities. Original stones (and *Fucus* for *J. praehirsuta*) were used as substrates though they were first washed in distilled water. The salinities used were 100, 80, 50, 30 and 5% sea waters, which were made up by diluting double-filtered sea water with re-aerated distilled water. At Plymouth outside sea water was used (35.1‰) and at Swansea aquarium sea water was used, the salinity varying from 31‰ to 35‰, depending upon the time when the experiments were carried out. About 20 animals were placed in each salinity (1 l.) and left for 4 days in continuous white light, following Riegel (1959), Todd (1963), Wertz (1963), McLusky (1967) and Wilson (1970), and after some preliminary experiments with *J. albifrons*. Animals used in the experiment, for which the results are illustrated in Fig. 1, were transferred from 100% s.w. at 17.5 °C to 5% s.w. at 17.5 °C and the blood of

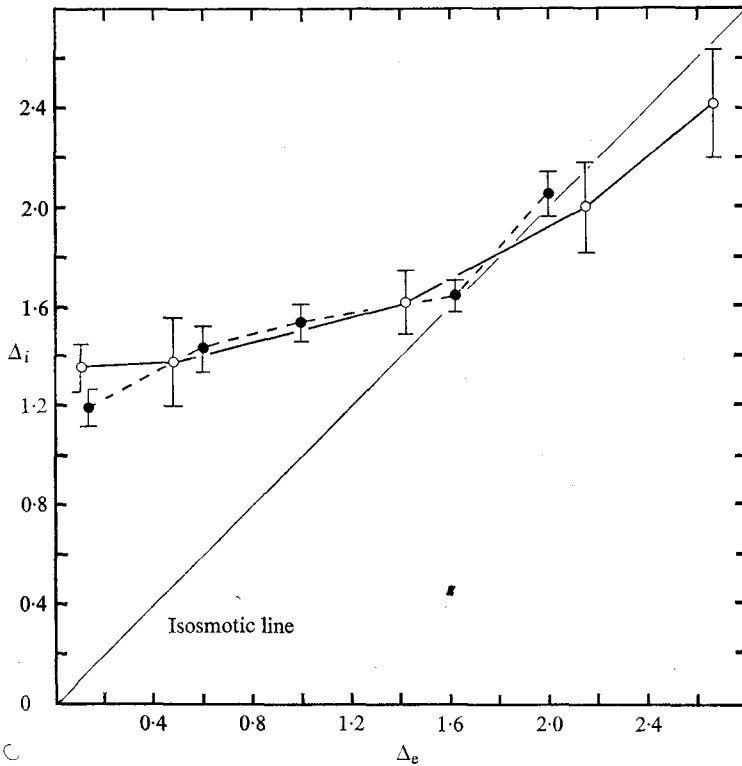


Fig. 2. Osmoregulation in *Jaera albifrons* at 8 °C (●) and 17.5 °C (○) plotted as mean Δ_i with standard deviations.

individuals was sampled after 3, 8, 24, 48 and 96 h. The results show that the animals acclimatized after only 3 h and this stable condition was maintained up to the end of the sampling period.

The method of blood collection is basically that of Ramsay & Brown (1955) except that the blood was taken directly from the heart (Parry, 1953; Lockwood, 1959; Werntz, 1963; Todd, 1963; Eltringham, 1964; Wilson, 1970). The blood samples were stored in a deep-freeze until they were observed on a modified Ramsay-Brown freezing-point determination apparatus (Ramsay & Brown, 1955) at the Plymouth Laboratory. Storage did not seem to affect the results as samples observed immediately after collection had the same freezing-point when recorded from the deep-freeze months later. Approximately ten animals were sampled in each salinity/temperature combination. The freezing-point depression in °C of the animal's body fluid is indicated by Δ_i and Δ_e refers to the external experimental medium which was sampled at the same time.

RESULTS

Jaera albifrons (Fig. 2)

At both temperatures (8° + 17.5 °C) *J. albifrons* regulates hyperosmotically in salinities below a freezing-point of -1.6 °C. Above this point it is isosmotic at 8 °C, but slightly hyposmotic at 17.5 °C. Between freezing-points of -1.6 and -0.6 °C the regulation at both temperatures is similar and the animals maintain a fairly stable internal osmotic pressure. At the lower end of the salinity range (-0.16 °C) the regulation at 17.5 °C is significantly higher than at 8 °C ($t = 3.656$, $P < 0.01$ for 11 D.F.).

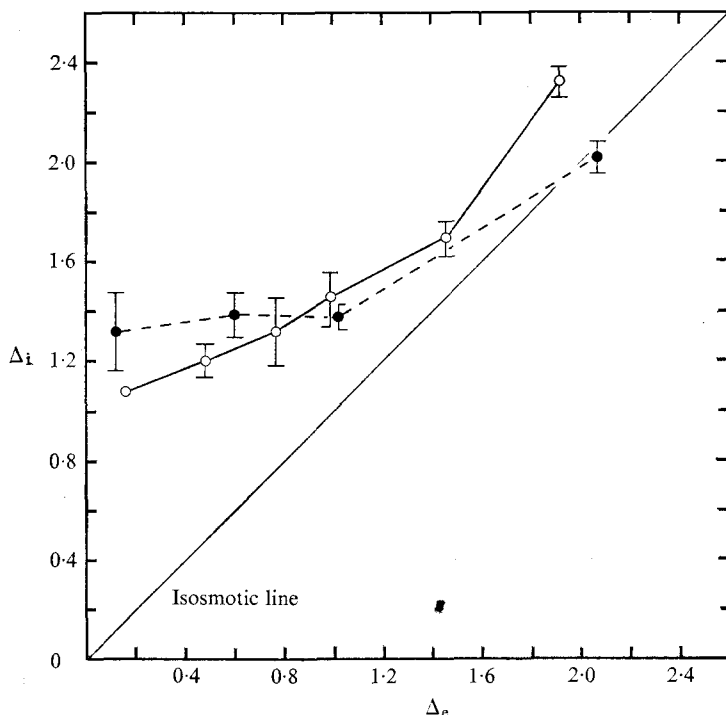


Fig. 5. Osmoregulation in *Jaera forsmanni* at 8 °C (●) and 15 °C (○) plotted as mean Δ_i with standard deviations.

Jaera ischiosetosa (Fig. 3)

In 100% s.w. *J. ischiosetosa* is slightly hyperosmotic at 17.5 °C and slightly hyposmotic at 8 °C. Below 100% s.w. the animals regulate hyperosmotically at both temperatures and maintain a fairly constant internal environment even in 5% s.w. At this low salinity (-0.12 °C) animals at 8 °C regulate significantly higher at the 5% level than those at 17.5 °C ($t = 2.239$, $P < 0.05$ for 16 D.F.).

Jaera praeheirsuta (Fig. 4)

J. praeheirsuta is isosmotic in 100% s.w. and 80% s.w. at both temperatures (8° + 17.5 °C), but below these salinities it regulates hyperosmotically. The regulation is not as high as seen in *J. albifrons* (Fig. 2) and *J. ischiosetosa* (Fig. 3) and at 17.5 °C seems to be in two stages. Between -2.0 and -1.0 °C the animals are hyperosmotic but the blood pressure falls, to some extent with decreasing salinity. Between -1.0 and -0.6 °C there is a more stable regulation but below -0.6 °C the internal osmotic pressure falls sharply.

Jaera forsmanni (Fig. 5)

J. forsmanni is a much less common species than the other three and fewer animals were available for the experiments. As a result only one animal was sampled from 5% s.w. at 15 °C compared with the other distributions on the graph which are based on the results from about six animals. In 100% s.w. at 8 °C *J. forsmanni* is slightly hyposmotic but below this it regulates hyperosmotically. However, there is a considerable drop in internal

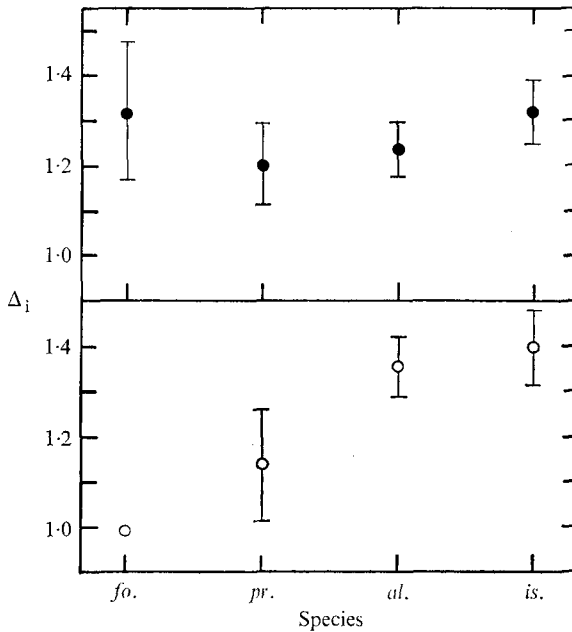


Fig. 6. The internal blood osmotic pressure of each species in 5% s.w. at 8 °C (●) and 17.5 °C (○) plotted as mean Δ_i with standard deviations (*J. forsmanni* was recorded at 15+8 °C).

osmotic pressure from 100% s.w. to 50% s.w. (-1.0 °C). Below -1.0 °C the blood pressure is maintained at a stable level with a decrease in 5% s.w. In 100% s.w. at 15 °C the animals are strongly hyperosmotic but below this the regulation curve conforms to the salinity curve although the blood is still maintained hyperosmotically.

DISCUSSION

Perhaps because of their large size, most of the work on osmoregulation in the Crustacea has been directed towards the Decapoda (see, for example, Robertson, 1960; Lockwood, 1962, 1968; Potts & Parry, 1964; Schoffeniels & Gilles, 1970; Hagerman, 1971). With the development of methods for use with small volumes of body fluid (Ramsay, 1949; Ramsay & Brown, 1955) some work has been carried out on isopods (Lockwood, 1959; Riegel, 1959; Frankenberg & Burbank, 1963; Todd, 1963; Eltringham, 1964; Wilson, 1970), but the information on these animals is still very scanty. The *J. albifrons* group of species is useful for such studies because it contains forms which occur in sea water, estuarine water, and almost fresh water (Naylor & Haahtela, 1966; Jones & Naylor, 1971). This present work provides complementary physiological evidence to the observed ecological differences in habitat preferences, and supplements observations on the differing rates of survival of each species at various salinities (Jones, 1972).

Each of the *Jaera* species has a similar pattern of osmoregulation in most of the salinities studied (Figs. 2-5). However, at 5% s.w. differences occur which can be directly related to the known ecological data. At 17.5 °C *J. ischiosetosa* has a significantly higher blood osmotic pressure than *J. prae-hirsuta* and *J. forsmanni*, but a very similar internal

TABLE 1. THE BLOOD OSMOTIC PRESSURE OF EACH *JAERA* SPECIES AT 17.5 °C IN 5% s.w.

(*J. forsmanni* recorded at 15 °C.)

Species of <i>Jaera</i>			
<i>ischioetosa</i>	$t = 0.3988$ $P > 0.1$ (D.F. = 15)		
<i>forsmanni</i>	$t = 3.658$ $0.02 > P > 0.01^*$ (D.F. = 6)	$t = 2.6336$ $0.05 > P > 0.02^*$ (D.F. = 10)	
<i>praehirsuta</i>	$t = 4.43$ $P < 0.001^{**}$ (D.F. = 12)	$t = 2.782$ $0.02 > P > 0.01^*$ (D.F. = 15)	$t = 0.446$ $P > 0.01$ (D.F. = 6)
Species	<i>albifrons</i>	<i>ischioetosa</i>	<i>forsmanni</i>

* Significant at the 5% level; ** significant at the 1% level.

TABLE 2. THE BLOOD OSMOTIC PRESSURE OF EACH *JAERA* SPECIES AT 8 °C IN 5% s.w.

Species of <i>Jaera</i>			
<i>ischioetosa</i>	$t = 2.8947$ $0.02 > P > 0.01^*$ (D.F. = 13)		
<i>forsmanni</i>	$t = 1.3990$ $P > 0.1$ (D.F. = 10)	$t = 1.2356$ $P > 0.1$ (D.F. = 11)	
<i>praehirsuta</i>	$t = 1.0786$ $P > 0.1$ (D.F. = 11)	$t = 2.851$ $0.02 > P > 0.01^*$ (D.F. = 12)	$t = 0.2155$ $P > 0.1$ (D.F. = 9)
Species	<i>albifrons</i>	<i>ischioetosa</i>	<i>forsmanni</i>

* Significant at the 5% level.

blood pressure to *J. albifrons* (Table 1; Fig. 6). This correlates with the occurrence of *J. albifrons* and *J. ischioetosa* in less stable conditions of salinity than *J. praehirsuta* and *J. forsmanni* (Naylor & Haahtela, 1966; Jones & Naylor, 1971). There is no significant difference between the osmoregulation of *J. forsmanni* and *J. praehirsuta* at this temperature and salinity combination (Table 1; Fig. 6). At 8 °C and 5% s.w. *J. ischioetosa* regulates significantly higher than *J. albifrons*, as might be expected from the ecological data, but the observation that *J. ischioetosa* and *J. forsmanni* regulate to a similar extent (Table 2; Fig. 6) is difficult to interpret unless, as seems likely, it reflects the small numbers of *J. forsmanni* which were available for the experiments.

Differing salinity tolerances seem to separate *J. ischioetosa* and *J. albifrons* from the other two *Jaera* species, while low temperature decreases the ability of *J. albifrons* to osmoregulate in dilute sea water (Tables 1, 2; Fig. 6). *J. praehirsuta* and *J. forsmanni* are therefore confirmed as the most marine species of the *J. albifrons* group, both showing lower osmoregulatory capacity than *J. albifrons* and *J. ischioetosa*. *J. forsmanni* at 15 °C has a very hyperosmotic blood pressure in 100% s.w. and in this respect seems physiologically similar to the semi-terrestrial isopod, *Ligia oceanica* (L.) (Parry, 1953; Todd, 1963). In this regard it is of interest that *Jaera forsmanni* is typically found beneath stones on parts of

the beach which may virtually dry out at low tide. Present physiological evidence therefore confirms earlier ecological observations on the *Jaera* species complex and suggests how genetic isolation between the various species is maintained. Further work on the ionic regulatory process of the four species would be worth while.

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