

OSMOREGULATORY CAPACITIES IN DISJUNCT WESTERN ATLANTIC POPULATIONS OF THE *SESARMA RETICULATUM* COMPLEX (DECAPODA: GRAPSIDAE)

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ABSTRACT

Osmotic and ionic regulatory capacities of a population of *Sesarma reticulatum* from Brunswick, Georgia, on the Atlantic coast of the United States were compared with those of a population of *S. sp.* (near *reticulatum*) from coastal Louisiana in the northern Gulf of Mexico. Samples of similar-sized adults from both populations were subjected to simultaneous 8-day acclimation treatments over a range of salinities from 48–1 ppt. At acclimation salinities from >5 to <35 ppt, animals from the northern Gulf of Mexico hyperosmoregulated at a lower plateau of blood osmolality than did those from the Atlantic coast. However, from midrange to the lowest acclimation salinities, hyperosmotic regulation in the Gulf of Mexico population was maintained without measurable reduction of blood osmotic concentration. A major component of the variation in blood osmolality appears to be reflected in differential regulation of sodium at salinities <10 ppt. We suggest that divergence in osmoregulatory pattern of sibling populations is genetically based and is maintained by the absence of gene flow around the peninsula of Florida. This divergence may reflect differential adaptation to habitats that vary in salinity structure, tidal effects, and temperature.

Coastal warm-temperate populations of decapods in the western Atlantic were long thought to be comprised of widely distributed species ranging from the Carolinian Province of the Atlantic coast into the northern Gulf of Mexico (Felder, 1973; Powers, 1977; Williams, 1984). However, recent studies of decapod crustaceans and other marine invertebrates in this region have shown some species complexes to possess distinct genetic discontinuities around the Florida Peninsula (Bert, 1986; Saunders *et al.*, 1986; Reeb and Avise, 1990). This genetic differentiation is evident not only in morphology and ecology of decapod crustaceans, but may be manifest also in unique physiological adaptations of separated populations (Williams and Felder, 1986).

While such physiological variation may be subtle, it can be evaluated by carefully controlled comparative experimentation. In the present study we have undertaken such a comparative investigation of osmotic and ionic regulatory capacities in what appear to be disjunct sibling populations of a coastal marsh crab, separated by the southern extreme of the Florida Peninsula. Under the label *Sesarma reticulatum* (Say, 1817), this species complex has been reported to range from Massachusetts to Volusia County, Florida, on the Atlantic coast and from Sarasota County, Florida, to Calhoun County,

Texas, in the Gulf of Mexico (Williams, 1984). Collections by one of us (DLF) extend the southern range of Gulf of Mexico populations well into Tamaulipas, Mexico.

Prior to studies by Zimmerman and Felder (1991), work concerning ecology, development, and physiology of this complex was focused almost exclusively on Atlantic coast populations (Crichton, 1960, 1974; Mulstay, 1975; Foskett, 1977; Seiple, 1979, 1981; Seiple and Salmon, 1982, 1987; Staton and Sulkin, 1991). However, recent work in our laboratory has established that Gulf of Mexico populations, while closely related to *S. reticulatum*, are distinct morphologically (Felder and Zimmerman, in preparation) and genetically (Felder and Staton, in preparation) from their Atlantic counterparts. In the present paper, we compare the osmotic and ionic regulatory capacities of adult marsh crabs from coastal Louisiana in the northern Gulf of Mexico, hereafter referred to as *Sesarma sp.* (near *reticulatum*), with those of *S. reticulatum* from the coast of Georgia on the Atlantic coast.

MATERIALS AND METHODS

All specimens used in experimental studies were adult crabs collected during the first week of August 1991. Animals were excavated by shovel at low tide from galleries in vegetated banks of tidal streams. Immediate pre- or postmolt animals and any animals injured during collecting were discarded from the samples. All

specimens of *Sesarma reticulatum* were taken from a salt marsh (*Spartina* and *Juncus*) subject to large tidal ranges at Brunswick, Georgia; salinity of adjacent waters at the time of collection ranged from 15–18 ppt. All specimens of *Sesarma* sp. (near *reticulatum*) were collected from brackish to fresh marsh (*Sagittaria*, *Scirpus*, and *Vigna*) subject to low tidal ranges near Cypermort Point, Louisiana; salinity of adjacent waters at the time of collection ranged from 3–8 ppt. Animals were transported to the laboratory in buckets of damp mud and vegetation from the collection site. Simultaneous acclimation of specimens from both populations was begun within 48 h of collection. Specimens from both populations were acclimated side by side under completely uniform conditions.

Initial acclimation attempts with animals of both populations produced high first-day mortality among animals that were grouped together without cover in a common container, usually from aggressive encounters between individuals that resulted in crushed appendages and blood loss. Thereafter, in order to acclimate animals together but without injury, each individual was isolated in a perforated plastic vial for the remaining term of acclimation. Acclimation waters were well aerated and could flow freely in and out of the perforated vials. Animals were maintained on a 12:12 h light : dark cycle at a temperature of $25 \pm 0.5^\circ\text{C}$, and were not fed during the full course of acclimation. Dilutions of filtered natural sea water were used for all acclimation salinities from 25–1 ppt. Salinities >25 ppt were obtained by dilution of a stock 50-ppt seawater solution prepared by addition of artificial sea salts to filtered natural sea water. All dilutions were made with deionized, dechlorinated water. Salinities of acclimation waters were approximated with a refractometer.

Animals were introduced into sea water of 25-ppt salinity and held there for 36–48 h before acclimation transfers were begun. Groups of animals were thereafter transferred stepwise in no more than 5-ppt increments or decrements per day, until the target acclimation salinity was reached. Target acclimation salinities were approximately 48, 35, 25, 15, 10, 5, and 1 ppt. Crabs were maintained at the target acclimation salinity for at least 8 days before blood was sampled. The maximum acclimation period (inclusive of initial holding at 25-ppt salinity, stepwise transfers, and final holding at the target salinity) was 16 days. Each specimen was acclimated to only one target salinity in the course of the experiment and was discarded after blood was sampled.

Blood was obtained by puncture of the arthroal membrane just proximal to the coxa of the fourth or fifth pereopod. Replicate 10- μl samples of blood and acclimation media were taken for determination of osmolality on a Wescor vapor pressure osmometer (Model 5100B). When possible, a third 10- μl whole-blood sample was obtained and immediately diluted for ion analysis. Replicate 10- μl samples of media were also taken and diluted for ion analyses. Chloride ion concentration was determined with an Aminco chloride titrator, and sodium ion concentration was determined with a Coleman (Model 21) flame photometer.

Replicate determinations of any blood sample were averaged to yield a single value. Values were thereafter used in calculation of means and 95% confidence intervals (CI) for sets of animals at each acclimation salinity. An unpaired *t*-test for small sample sizes (So-

kal and Rohlf, 1981: 226) was used to evaluate the level of significance for any difference between means.

RESULTS

Both *S. reticulatum* from Georgia and *S. sp.* (near *reticulatum*) from Louisiana survived all acclimation treatments. Neither population demonstrated a lower or higher lethal limit at target acclimation salinities during the study. Overall, mortality during acclimation was less than 4% for the Louisiana population and less than 2% for the Georgia population during the final 8 days of acclimation. This rate was substantially lower than in the first day of early trials when acclimation of animals was attempted without use of isolation vials, and mortality during a single day for animals from both populations exceeded 12%.

Both *S. reticulatum* and *S. sp.* (near *reticulatum*) exhibit in general a type IV osmoregulatory curve (sensu Vernberg and Vernberg, 1972) typical of grapsid crabs that are strong euryhaline osmoregulators (Mantel and Farmer, 1983). Weak hypoosmotic regulation is evident at salinities >25 ppt (Fig. 1), with no significant difference in this pattern between the two populations; at acclimation salinities from 35–48 ppt, blood osmotic concentration parallels changing acclimation salinity in both populations. However, at midrange salinities (25–10 ppt), animals from the Georgia population maintained blood osmotic concentrations slightly but significantly ($P < 0.001$) higher than did those from the Louisiana population. Overall, hyperosmotic regulation of the blood between 25–1 ppt was maintained on a relatively stable plateau in both populations, though blood osmotic concentration decreased to slightly but significantly ($P < 0.01$) lower values at the lowest acclimation salinities in the Georgia population. No significant reduction in blood osmolality occurred in the Louisiana population from 15 ppt to the lowest acclimation salinity of 1 ppt. Rather, a very slight but significant ($P < 0.05$) increase in blood osmolality occurred with the decrease of acclimation salinity from 15–5 ppt; a similar pattern of significant ($P < 0.02$) increase in mean blood ion values also occurred over this reduction of acclimation salinity (Figs. 2, 3).

Regulation patterns for both sodium (Fig. 2) and chloride (Fig. 3) were very similar to

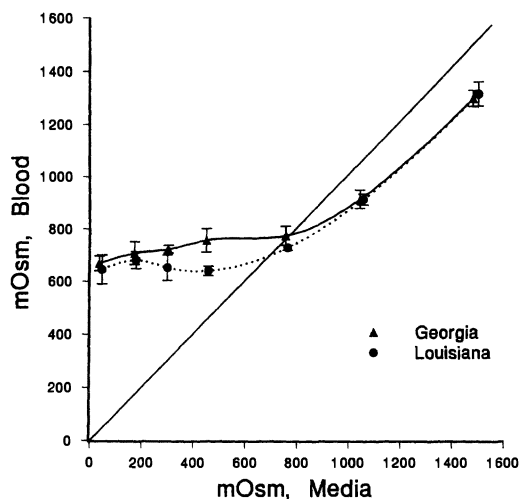


Fig. 1. Blood osmotic concentration in acclimated specimens of *Sesarma reticulatum* from Georgia (triangles) and *Sesarma* sp. (near *reticulatum*) from Louisiana (circles) as a function of varied osmotic concentration in acclimation media. Each point is mean for 4–8 animals acclimated at $25 \pm 0.5^\circ\text{C}$; vertical bars indicate 95% CI. Isosmotic line is shown as diagonal. Media osmolalities from lowest to highest correspond to acclimation salinities of 1, 5, 10, 15, 25, 35, and 48 ppt.

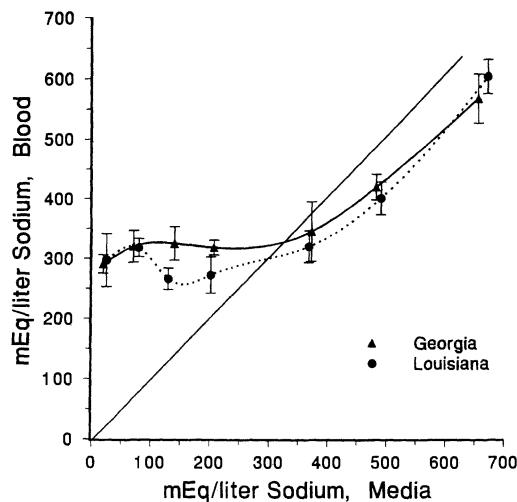


Fig. 2. Blood sodium concentration in acclimated specimens of *Sesarma reticulatum* from Georgia (triangles) and *Sesarma* sp. (near *reticulatum*) from Louisiana (circles) as a function of varied sodium concentration in acclimation media. Each point is mean for 3–8 animals acclimated at $25 \pm 0.5^\circ\text{C}$; vertical bars indicate 95% CI. Isoionic line is shown as diagonal. Media sodium concentrations from lowest to highest correspond to acclimation salinities of 1, 5, 10, 15, 25, 35, and 48 ppt.

the pattern for overall osmotic concentration. In both cases, blood ion levels at mid-range acclimation salinities in the Louisiana population were slightly but significantly ($P < 0.01$) below those in animals from the Georgia population. However, at the lowest acclimation salinities (5 and 1 ppt) values for blood sodium and chloride ion concentrations in animals from the Louisiana population recovered to values that approximated those for animals from the Georgia population. In the population from Georgia, concentrations of blood chloride and sodium were both slightly but significantly ($P < 0.02$) lower at the minimum acclimation salinity (1 ppt) than at an acclimation salinity of 25 ppt. In animals from the Louisiana population, there was no significant difference in blood ion concentrations between animals acclimated to 25 ppt and those acclimated to 1 ppt.

DISCUSSION

The results of this study suggest a subtle physiological divergence, measurable in osmoregulatory ability, between Gulf of Mexico and Atlantic populations of the *Sesarma reticulatum* complex. While the osmotic and

ionic regulatory patterns reported here for both populations agree in general with patterns of osmotic and ionic regulation reported in previous studies of *S. reticulatum* by Foskett (1977) and in some studies of other grapsid crabs (Gross, 1964; Barnes, 1967; Mantel and Farmer, 1983), the direct comparison of closely related Gulf and Atlantic populations establishes small but consistent differences in magnitude of response when animals are acclimated to a range of estuarine salinities. Our measures of osmotic and ionic regulation demonstrate ability of individuals from the Gulf of Mexico to regulate blood homeostatically, but at a lower plateau than those of the Atlantic. Such differences in osmoregulation are often found with species-level comparisons of physiology (Mantel and Farmer, 1983) and are usually attributed either to localized environmental conditioning (phenotypic compensation) of genetically homogeneous populations or to genetic divergence (adaptation) of isolated populations (see Vernberg, 1962).

Effects of local, long-term environmental conditioning are difficult to document with certainty as such in geographically separat-

ed populations, especially in the absence of genetic analyses. In at least some cases, variant physiological responses attributed to long-term conditioning across latitudinal gradients in temperature or other parameters may just as readily correlate with measures of genetic divergence, once genetic or other systematic data become available. In many cases, divergent physiological responses have been portrayed as conditioning effects without either genetic analyses or even rigorous morphological comparison of the specimen populations under study. However, this is not to say that climate, nutrition, ontogeny, and other conditioning of osmoregulatory response do not occur among coastal decapods, and it is probably some synergism of these that leads to seasonal variation of osmoregulatory capacity in coastal populations such as grapsid crabs (Dehnel, 1962), portunid crabs (Mantel, 1967; Ballard and Abbott, 1969), and callicianassid mud shrimp (Felder, 1978). To control as much as possible for such effects in the present study, population samples from Louisiana in the Gulf of Mexico and Georgia on the Atlantic coast were taken from within 1° of the same latitude (30–31°N). As further control, both samples were taken at the same time of year, both were restricted to the same maturational stages, both were held in the laboratory for the same period of time, and both were acclimated under identical experimental conditions at the same time.

In the case of the *S. reticulatum* complex, some disparity in the typical habitat between the Atlantic and Gulf of Mexico populations may serve to account for divergence in osmoregulatory ability observed in the present study, regardless of whether it is environmentally conditioned or genetically based. The Georgia population, typical of the Atlantic coast populations in general, is subject to a much higher tidal amplitude and at least periodically higher salinities than are most populations in the Gulf of Mexico. *Sesarma reticulatum* on the Atlantic coast is reported to range from salinities <2 to >35 ppt, but it appears to prefer a mean salinity of about 16 ppt (Seiple, 1979). However, *S. sp.* (near *reticulatum*) ranges from salinities of <1 ppt to (occasionally) >40 ppt in the Gulf of Mexico, and the largest populations are found from 1–15 ppt (Zim-

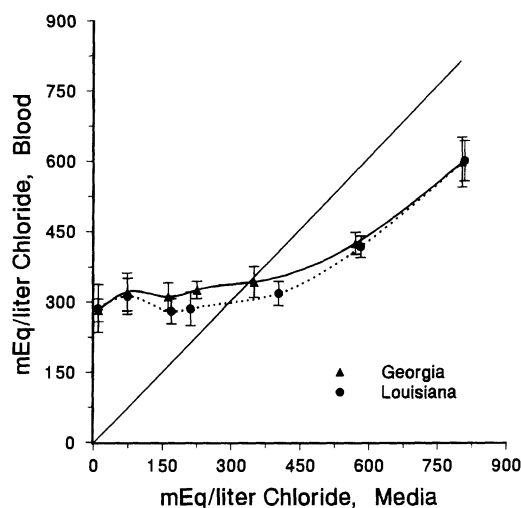


Fig. 3. Blood chloride concentration in acclimated specimens of *Sesarma reticulatum* from Georgia (triangles) and *Sesarma sp.* (near *reticulatum*) from Louisiana (circles) as a function of varied chloride concentration in acclimation media. Each point is mean for 3–8 animals acclimated at $25 \pm 0.5^\circ\text{C}$; vertical bars indicate 95% CI. Isoionic line is shown as diagonal. Media chloride concentrations from lowest to highest correspond to acclimation salinities of 1, 5, 10, 15, 25, 35, and 48 ppt.

merman and Felder, 1991); most of these populations experience annual mean salinities of about 7 ppt. Thus, populations in the Gulf of Mexico appear to center in habitats of lower mean salinity than those of the Atlantic, and, given the lower tidal amplitude throughout most of the range in the Gulf of Mexico, these populations are less likely to experience periodic inundation by higher salinity waters carried into upper estuaries with high tides.

There are also disparities in overall habitat temperature ranges and means between the Atlantic and Gulf of Mexico populations, and long-term conditioning to these differences may influence osmoregulatory patterns beyond the habitat and climate effects that can be controlled for simply by selecting test samples from similar latitudes (see above). Assuming that populations on the Atlantic coast represent one genetically similar clade and that populations in the Gulf of Mexico represent another, it is apparent that mean temperatures of the Atlantic range (Massachusetts to Volusia County, Florida) are presently, and have been historically, lower than within the Gulf

of Mexico range (Sarasota County, Florida, to Tamaulipas, Mexico). Although there are certain exceptions to the general pattern, higher temperatures appear to both reduce optimum blood osmotic concentrations and increase the range of tolerance to lowered salinity in brackish water animals. This observation has been interpreted previously as a physiological reason for adaptation to brackish water being favored in warm water environments (see review by Vernberg, 1962). The influence of higher temperature on sodium ion transport may also assist some species in the invasion of more dilute media (Lockwood, 1960).

A somewhat different pattern of blood sodium ion regulation is seen in the Gulf of Mexico population from that in the Atlantic population, and this may reflect some fundamental difference in response to extreme low salinities in these two groups. In the Louisiana population, a measured increase in sodium ion levels at the 5-ppt acclimation salinity cannot be attributed casually to artifact, since it is also detected in the independent determination of total osmolality and appears to be reflected in the independent measure of blood chloride ion. Rather, the transition from an acclimation salinity of 10 ppt to 5 ppt may be coincident with greater saturation of the sodium active transport process. This could at least in part account for "recovery" of blood osmotic concentration at low salinities in *S. sp.* (near *reticulatum*) to equivalency with that of *S. reticulatum*. By contrast, saturation of sodium transport could have occurred at a higher salinity for *S. reticulatum* which showed no similar recovery point but rather exhibited a tendency for slight attenuation of blood osmotic concentration to lower values as salinity decreased.

A selective advantage of such disparate patterns could relate to differing salinity regimes of the two populations. In the lower salinity habitats of the Gulf of Mexico, *S. sp.* (near *reticulatum*) may achieve some energetic advantage by functioning at a lower plateau of blood osmotic concentration; for example, reserve capacity for sodium transport appears to be activated only at the lowest salinity extremes of the typical habitat. In habitats where salinity may average 3–4 ppt, these animals could behaviorally avoid long-duration exposure to low salinity ex-

trêmes by limiting incursions into low salinity waters as might persist during low tides. Even under some conditions where high tides may increase levels of low salinity waters along inhabited banks of tidal streams, the tidal range is often so low as to leave extensive areas of the burrow galleries unflooded. Thus, the semiterrestrial habits of these animals could serve as a means of avoiding direct and prolonged exposure to extremely low salinity under most circumstances. However, under forced continual exposure to extreme low salinity, as imposed in our acclimation protocols, compensational sodium transport ability may be triggered, accounting for the observed "recovery" and restabilization in blood osmolality at salinities from 5–1 ppt. In contrast, *S. reticulatum* on the Atlantic coast appears to saturate sodium transport ability at a higher salinity, such as may be expected in a population centered in higher salinity habitats and in localities where moderate to high tidal ranges periodically bathe even upper estuaries with more saline waters. Confirmation of the role of sodium transport in the divergent patterns observed will require more direct measurement of transport rates and investigation of possible variations in factors such as urine production and permeability. Acclimation over periods longer than used in the present study may also be required in order to determine whether the two populations maintain divergent patterns of sodium regulation over the long term.

In one of the very few previous comparisons of osmoregulation between Gulf of Mexico and Atlantic coast decapod crustacean populations, Sharp and Neff (1980) noted that populations of *Clibanarius vittatus* from coastal Texas were not different in osmotic and ionic regulatory ability from those in South Carolina (Young, 1979). However, despite the wide separation of the populations sampled, there is no evidence to date that those populations are genetically divergent, and the species appears to range fully around the peninsula of Florida (DLF, unpublished records). The salinity structure of the typical habitat in *C. vittatus* does not appear to vary appreciably between the populations evaluated. Rather, more typical of those shallow subtidal warm-temperate taxa that are not disjunct across

the Florida Peninsula, *C. vittatus* exhibits some degree of "brackish water submergence" (sensu Remane and Schlieper, 1958) over its range. That is to say, *C. vittatus* occupies extensively the upper littoral environments and marshes of coastal estuaries on the Atlantic coast, while it is more restricted to saltier margins of marshes, bay shores, and sublittoral waters in the northern Gulf of Mexico, where lower salinity waters bathe expansive marshes of upper estuaries. By contrast, brackish water submergence would not be expected in obligate intertidal animals such as the *Sesarma reticulatum* complex; rather, a genetically distinct counterpart of *S. reticulatum* (sensu stricto) appears to have become adapted to the expansive, low-salinity marshlands of the northern Gulf of Mexico, perhaps in response to a suite of environmental factors.

Powers and Place (1978) delineated two potential modes of such genetic change in populations: the "ongoing" model that is based on adaptation and nonrandom migrational processes, and the "historical" model that requires previous genetic isolation to produce differentiation. Although our data do not allow us to argue exclusively for either pattern of differentiation, limitation of gene flow in the *S. reticulatum* complex (as suggested by allozyme differences; our unpublished data) could allow for allopatric divergence in physiological as well as allozymic composition of these populations. Even though the Florida Peninsula serves as a well-documented biogeographic and genetic boundary between coastal Atlantic and Gulf of Mexico fauna, the ultimate cause of differentiation in these faunal regions may be complex. North American glaciations, pluvial runoff, and expansion of deltaic wetlands during the Quaternary all served to develop the modern physiographic character of estuaries and wetlands in the Gulf of Mexico. The modern coastal fauna of the northern Gulf of Mexico, of which *S. sp.* (near *reticulatum*) is a part, may demonstrate a unique physiology adaptive to this physiographic zone.

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