

Combined Effects of Temperature and Salinity on Larval Development of the Mangrove Crab *Parasesarma catenata* Ortman, 1897 (Brachyura: Sesarmidae)

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Abstract—The larval stages of the mangrove crab *Parasesarma catenata* were reared in the laboratory from eggs of females collected in the Mgzana estuary, South Africa. Survival and duration of larval stages were tested for the combined effects of temperature and salinity in a factorial design experiment, using three females each with two replicates of 15 larvae per combination. Combinations were made from five temperature (15, 20, 25, 30 and 35 °C) and four salinity values (15, 25, 35 and 45 ‰). Results were tested by ANOVA and multiple regression was applied to generate contour models by polynomial equation. It was found that *P. catenata* larvae develop optimally in near to seawater salinity at a temperature of around 25 °C. These results support the assumption that newly-hatched larvae of this species are exported from the estuarine environment to the sea for development.

INTRODUCTION

Tropical mangrove habitats are generally brackish water environments, and have endemic brachyuran species most of which show an ‘exportation’ life cycle strategy (e.g. Dittel et al., 1991; Paula et al. 2000), as found in estuaries in general (Queiroga, 1996). Newly-hatched larvae immigrate by passive and active mechanisms to adjacent shelf waters, using selective stream tidal transport (Queiroga et al., 1997; Queiroga, 1998). This mechanism is thought to be important for avoidance of estuarine environmental stress and high predation pressure (Paula, 1989). The variability of water masses, which affects larvae during development, may have a major impact on their survival, transport and ultimately recruitment success.

One of major factors accounting for estuarine

stress is salinity, as osmoregulatory capability develops throughout the larval sequence of stages (Charmantier, 1998), and most newly-hatched stages are regarded as being more sensitive to low salinity (Charmantier et al., 2002). However, in some freshwater species hatching occurs in freshwater with subsequent seaward exportation, and in this case the newly-hatched stage has strong osmoregulation capability (Charmantier et al., 1998). Within a tolerated range, temperature mostly affects duration of larval stages, and these effects in turn affect dispersal and gene flow interacting with coastal physical processes (Crisp, 1976). Larval survival is thus strongly affected by temperature and salinity (Sandifer, 1973; Paula et al., 2001a), although each species’ tolerance will be specific for its degree of adaptation to the environmental gradients of coastal systems.

Sesarmid crabs, one of major crustacean families in mangrove systems, occupy a wide diversity of aquatic habitats from nearly marine to freshwater. Their adaptation to different and often varying-salinity environments has resulted in a gradient of osmoregulatory capabilities and life cycle strategies in the crabs. The effects of temperature and salinity on larval development of sesarmid crabs have been studied in a number of species, such as *Sesarma cinereum* (Costlow et al., 1960), *S. rectum* (Fransozo & Negreiros-Fransozo, 1986), *Aratus pisonii* (Diaz & Bevilacqua, 1986), *S. angustipes* (Anger et al., 1990), *S. recordi* (Alvarez & Ewald, 1990), *S. reticulatum* (Paula et al., 1992), *Armases miersii* (Schuh & Diesel, 1995a), *S. curacoense* (Schuh & Diesel, 1995b), *Arm. ricordi* and *Arm. roberti* (Diesel & Schuh, 1998).

Parasesarma catenata is one of the most common species of estuarine marsh crabs in southern Africa, with a distribution extending from the Bree River to Inhaca Island, Mozambique (Kensley, 1981; Day, 1981). In southern Cape estuaries it is found in high densities within *Spartina* salt-marshes, while in the Transkei, Kwa-Zulu Natal and southern Mozambique this species is associated with mangrove swamps. Its larval development has four zoeal and a megalopa stage as described by Pereyra-Lago (1987). In the Mgazana estuary, South Africa, the breeding season for *P. catenata* starts around August (Emmerson, 1994), and newly-hatched stages are effectively exported from the estuarine environment (Pereyra-Lago, 1993).

The objective of this work was to study the temperature and salinity effects on larval development of *Parasesarma catenata*, in relation to survival and duration of larval stages. To accomplish this aim, a factorial designed experiment was carried out in the laboratory under controlled conditions.

MATERIALS AND METHODS

Female collection

Ovigerous females of *Parasesarma catenata* were hand-collected in the mangrove swamp among *Avicennia marina* trees in Mgazana estuary, Transkei coast in South Africa. Ovigerous females were transported to the marine laboratory of

University of Transkei, Umtata. The crabs were maintained individually without food at 25 °C and at a salinity of 35 ‰ until hatching.

Experimental design

The experiment followed a factorial design, and combinations were made from five temperatures (15, 20, 25, 30 and 35 °C) and four salinities (15, 25, 35 and 45 ‰). In each combination 3 random females were used from a minimum set of 6 hatchings, each female with 2 replicates of 15 larvae. Larvae were chosen from amongst the most active of respective batches. Each replicate was cultured in 400 ml glass bowls. Water was periodically brought from the shore, and filtered through a series of Millipore filters down to 0.5 µm. Dilution was done using de-ionised water and concentration was obtained by evaporation. Temperatures were regulated in enclosed chambers to precision of within ± 0.5 °C.

Larvae were transferred to new cultures each day and fed on newly-hatched *Artemia nauplii*. While transferring, larvae were checked for mortality and sorted by developmental stage. At high temperatures (30 and 35 °C) the cultures were covered with adhesive plastic to prevent evaporation and consequent salinity increase. The experiment lasted until the juvenile stage was reached.

Temperature and salinity effects on survival of larval stages were tested by 2-way factorial ANOVA. Percent cumulative survival was transformed by angular transformation ($\arcsin \sqrt{\text{proportion}}$). Regression coefficients were used in the polynomial expression to generate a surface response contour (Box & Youle, 1955):

$$Z = b_0 + b_1T + b_2S + b_{11}T^2 + b_{22}S^2 + b_{12}TS$$

where Z is the surface response, T is temperature, S is salinity, b_0 is the multiple regression constant, b_1 and b_2 are the linear effects of temperature and salinity, b_{11} and b_{22} are the quadratic effects, and b_{12} is the intersection effect. No statistical test was applied to duration of larval stages, as total mortality in a number of extreme temperature and salinity combinations makes the planned comparisons highly unbalanced and of restricted interpretation value.

RESULTS

The cumulative sequence of larval stages obtained in the various temperature and salinity combinations is presented in Fig. 1. It is clear that for the tested ranges of temperature and salinity it is the latter which mostly affects the survival of the larval stages, especially at lower ranges. At the lowest salinity tested (15 ‰) and at the lower and higher temperature (15, 20 and 35 °C) combinations, complete mortality for stage I was obtained, with low survival for the next stages at 25 and 35 °C. At the lowest temperature (15 °C) and higher salinities (35 and 45 ‰), there were good survival rates for the zoeal stages, but no larvae reached the megalopa stage. The combinations which produced juvenile stages were between 20 and 30 °C and between 25 and 45 ‰ salinity. Duration to megalopa was shorter at 30 °C than at 20 and 25 °C, but survival rates were higher at 20 and 25 °C than at 30 °C.

Figure 2 presents the results of cumulative survival in the temperature and salinity combinations for each larval stage. For all zoeal stages the highest survival was obtained at 25 °C (with very similar results at 20 and 30 °C), with sea water salinity (35 ‰), but survival decreased towards the lower and higher values of the salinity tested. The lowest salinity (15) induced the lowest survival—nearly all first zoeal larvae died at all the temperatures tested.

The results of cumulative duration of larval stages were not consistent with the results obtained for survival, i.e. the optimal points for survival are not coincident with the highest developmental rate up to a certain degree (Fig. 3). The developmental rate at 30 °C was faster than at any other temperature, and this trend was consistent for all salinity values.

ANOVA results showed not only that both temperature and salinity have significant effects on survival for all larval stages (Table 1), but also

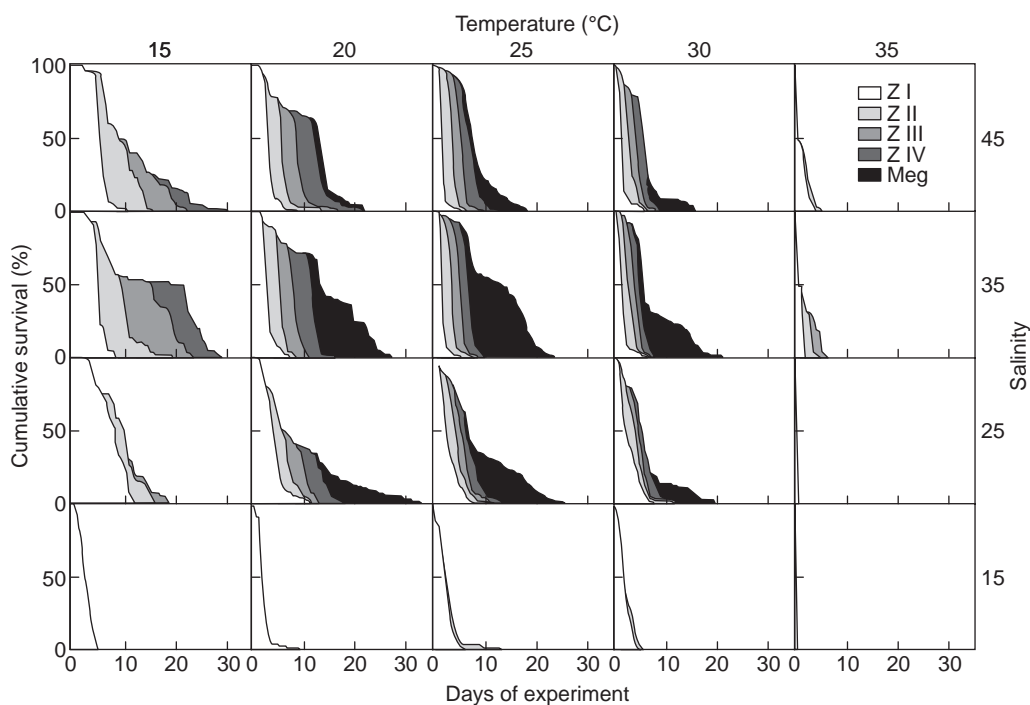


Fig. 1. Survival of sequence of developmental stages of *Parasesarma catenata* obtained in the temperature and salinity combinations. ZI to ZIV – zoeal stages I to IV, Meg – megalopa.

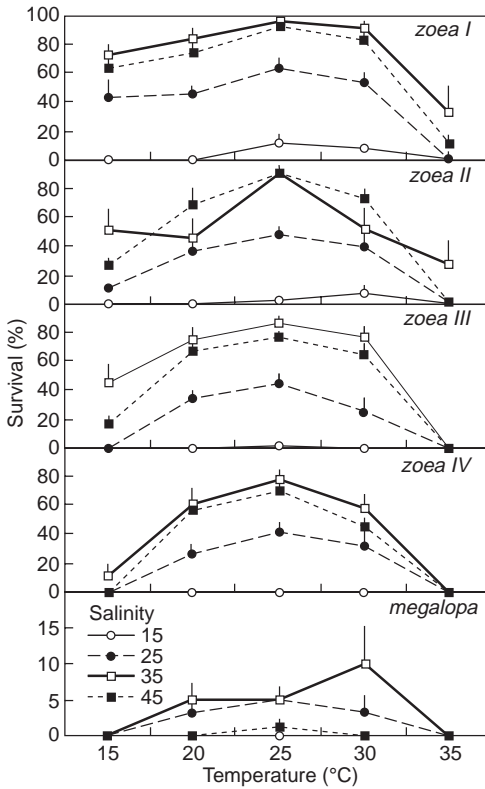


Fig. 2. Average cumulative survival of sequence of larval stages of *Parasesarma catenata* obtained in the temperature and salinity combinations. Error bars refer to standard error

Table 1. Results of a 2-way ANOVA for survival of zoeae I to megalopa *Parasesarma catenata* for salinity and temperature matrix. ZI–ZIV, zoeal stages I to IV; T, temperature; S, salinity

Source	MS	DF	F	P-level
ZI				
T	2.114	4	43.11	< 0.0001
S	5.465	3	111.48	< 0.0001
T x S	0.136	12	2.78	0.0027
ZII				
T	1.941	4	44.66	< 0.0001
S	4.590	3	105.63	< 0.0001
T x S	0.235	12	5.42	< 0.0001
ZIII				
T	2.184	4	62.56	< 0.0001
S	3.591	3	102.85	< 0.0001
T x S	0.283	12	8.11	< 0.0001
ZIV				
T	2.224	4	64.68	< 0.0001
S	2.068	3	60.12	< 0.0001
T x S	0.282	12	8.21	< 0.0001

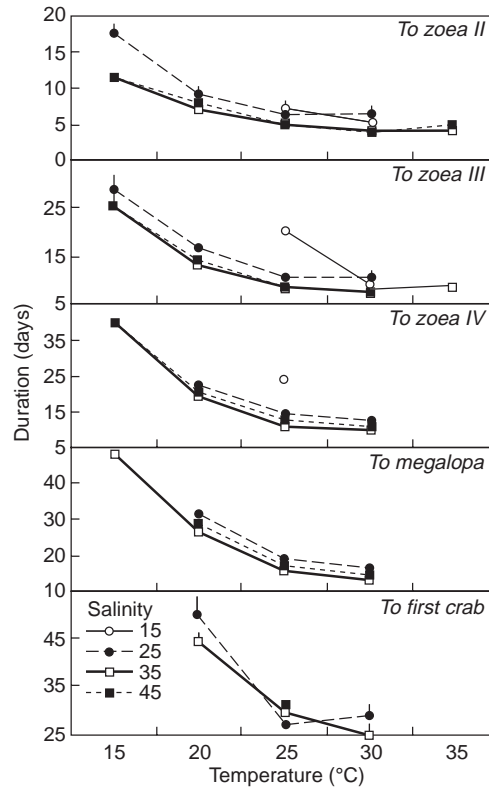


Fig. 3. Average cumulative duration of sequence of larval stages of *Parasesarma catenata* obtained in the temperature and salinity combinations. Error bars refer to standard error

their interaction. Overall the result of analysis of variance for mortality was a fully significant matrix for larval stages, factors and their interaction.

Contour analysis defines clear centres of optimal combinations of temperature and salinity for the survival of *Parasesarma catenata* larval stages (Fig. 4). The optimal points of salinity are close to full salinity seawater, and temperature is within the expected normal range for summer condition in the area (20 to 27 °C).

DISCUSSION

The larval stages of estuarine species, especially the megalopa, encounter a changing estuarine environment, especially in salinity, when migrating back to parental areas. Although their survival can physiologically be similar to the previous stages, the acceleration of the moulting process with a lowering in salinity can account for increasing

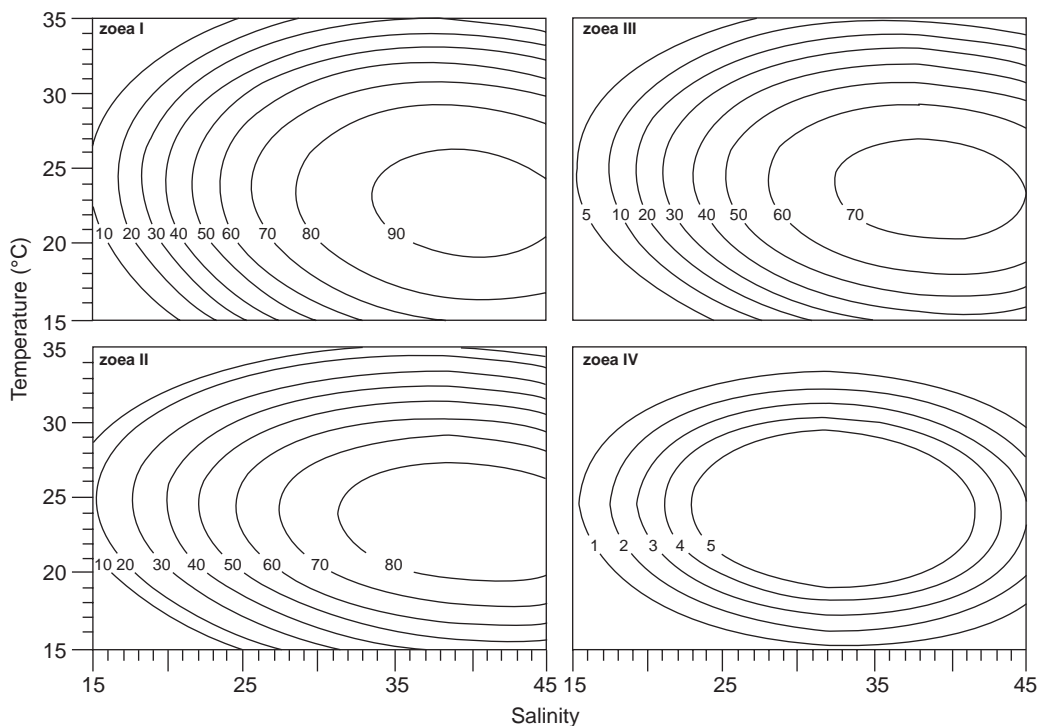


Fig. 4. Contour plots for survival of larval stages of *Parasesarma catenata* in the tested temperature and salinity matrix

survival. Several studies, however, refer to plasticity in the timing of moult for late larval stages (Sulkin & Van Heukelem, 1986; O'Connor, 1991), which can be an adaptation to the variability of coastal waters encountered by megalopae when returning to appropriate settlement areas.

In *P. catenata*, the optimal development was found at normal sea water salinity, but with a higher tolerance for increased salinity. The duration of larval development is shorter at higher than at lower temperatures. This could be an adaptation to summer conditions in coastal systems, such as the Mgazana estuary. This estuary is stratified at the mouth with marine conditions (Branch & Grindley, 1979), and during summer, the temperature is around 21 °C and salinity around 32 ‰ at the bottom of the estuary. Adult populations of *Parasesarma* inhabit the lower estuarine region, and the species has lower tolerance to decreasing salinity (Boltt & Heeg, 1975) than other sesarmid species.

Some species, such as *Sesarma caracaoense*, inhabiting mangroves, which are generally characterised by strong thermo-haline fluctuations at different temporal scales, show a wide range of

tolerance (Schuh & Diesel, 1995b). Some estuarine species, e.g. *Palaemonetes varians*, will maintain a wide tolerance throughout development (Antonopoulou & Emson, 1989), showing capacity of retention in the upper part of estuaries (Paula, 1998). In estuarine species, which show an obvious strategy of larval exportation from the estuarine boundaries, salinity tolerance is narrow, with optimal development being achieved in close to full sea water salinity (e.g. *Sesarma reticulatum*: Paula et al., 1992; *Carcinus maenas*: Nagaraj, 1993), as also evident in *P. catenata*.

The present results thus corroborate the estuarine exportation type of life cycle for *Parasesarma catenata*, as suggested by field results by Pereyra-Lago (1993) and Paula et al. (2000). Other decapod crustacean groups in East African mangroves present similar life cycle strategies (e.g. Wooldridge & Loubser, 1996). Larvae of several East African mangrove sesarmids have also been observed returning to parental areas from offshore (Paula et al., 2001b; 2003) as megalopal stages, strongly suggesting that most mangrove crabs have a neritic planktonic larval development.

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