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Effects of salinity and temperature on the larval development of a sesarmid crab *Neosarmatium trispinosum* Davie (Crustacea: Brachyura: Sesarmidae) from mangrove swamp in Okinawa Island, Japan

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Abstract
The larval development of the semiterrestrial sesarmid mangrove crab *Neosarmatium trispinosum* was studied under laboratory conditions at salinities 0-35‰ and constant temperatures of 20-30°C. The larval development consists of five zoeal stages and a megalopa. Larvae survived to the first crab stage at salinities between 15 and 35‰ with different percentages. At 0, 5 and 10‰, the larvae died within 12-18 hours without moulting to subsequent stages. The highest survival rate was recorded at 20-25‰ and 25-30°C with shortest development duration to the first crab stage ranging from 24-28 days. At the highest salinity (35‰), survival rate was gradually decreased with increasing development duration. There were significant differences ($P<0.01$) found in the development period among the tested salinities. Results of this study suggest that the larvae of *N. trispinosum* develop in estuarine water and recruit to the mangrove swamp at the megalopa stage, where they spend the rest of their lives.

Key words: Mangrove crab, *Neosarmatium trispinosum*, Larval development

Introduction

The crabs of the family Sesarmidae are important components of mangrove ecosystems in the Indo-West Pacific, Africa, the Caribbean and South America. By retaining a large proportion of mangrove leaf-litter within mangrove forests, they profoundly influence the functioning of mangrove ecosystems (Sheaves and Molony 2000). Crabs of the genus *Neosarmatium* are among the largest of the intertidal mangrove sesarmids (Ng *et al.* 1996). Among the recognised species, *N. trispinosum* is an uncommon species found in the mangrove swamps of southern Okinawa Island, Japan. *Neosarmatium trispinosum* builds large characteristic mounds at the entrance to its burrow. This species is also found in the mud flats between low and high tide marks, and mangrove areas (Sakai 1976, Dai and Yang 1991). The crab emerges from its burrow at

night to remove litter from the surface of the mud (Gaddins *et al.* 1986). This species is a major leaf consumer, carrying leaves into its burrow where they are allowed to age and decay prior to consumption (Gaddins *et al.* 1986, Neilson and Richards 1989).

N. trispinosum has long been confused with *N. smithi* (H. Milne Edwards 1853), from which it can be easily separated by the shape and position of the teeth on the upper margin of the dactyl of the male cheliped (Davie 1994). On *N. trispinosum* the three spines are acute, and placed close together in the proximal two-thirds; whereas in *N. smithi* they are truncate, and spaced out over the proximal half (Davie 1994).

Sesarmid crabs are frequent inhabitants of transitional habitats between marine intertidal and adjacent freshwater or terrestrial zones (Anger and Charmantier 2000). In most of these species, however, reproduction depends on an export of the larval stages into the ancestral environment, the sea, and later remigration of megalopae or benthic juveniles into the brackish or semiterrestrial parental habitats (Hartnoll 1988, Anger 1995, Anger and Charmantier 2000).

Salinity and temperature are among the most important physical factors in the life of marine and brackish water organisms (Browne and Wanigasekera 2000). There is often a complex co-relationship between the two factors, where temperature can modify the effects of salinity, thereby changing the salinity tolerance of an organism, and salinity can modify the effects of temperature accordingly (Kinne 1963, Browne and Wanigasekera 2000). Several published documents deal with the effects of a variety of salinity and temperature levels on the larval development of different species of sesarmid crabs (Costlow *et al.* 1960, Anger *et al.* 1990, Schuh and Diesel 1995a,b, Diesel and Schuh 1998, Islam *et al.* 2000, 2002a).

Prior to this study, larval development is known only for *N. fourmanoiri* (Islam *et al.* 2003), *N. indicum* (Islam *et al.* 2002b) and *N. meinerti* (Pereyra Lago 1989, as *Sesarma meinerti)* within the genus *Neosarmatium.* Their larval development consists of five zoeal stages and a megalopa under laboratory conditions. Considering the importance of these species in the mangrove ecosystem, we examined the influence of salinity and temperature on the larval development of *N. trispinosum.*

Materials and methods

An ovigerous *N. trispinosum* crab measuring 34 mm in carapace length and 37 mm in carapace width was captured by hand from a burrow in the Shimajiri mangrove swamp of Miyako Island (26°20'N-26°30'N, 128°10'E-128°20'E), southern Okinawa, Japan. The female was brought to the Laboratory of Fisheries Biology, University of the Ryukyus, Okinawa, and reared in a plastic container (32x18x22 cm) with 16±1‰ salinity, 28.5±0.31°C ambient temperatures and moderate aeration. The female was fed with "Tetra Fin" (small dry fish) and aged mangrove leaves. Seawater was changed daily until the eggs hatched. Hatching occurred after 18 days of rearing. The larvae were reared for mass culture under the same conditions as indicated for the ovigerous female.

The larvae were subjected to eight different salinity levels (0-35‰, by step of 5‰), measured with an Atago Hand Refractometer to the nearest 1‰, and three different

constant temperatures (20, 25 and 30°C). The above salinities were obtained by diluting filtered seawater with dechlorinated tap water. Temperature was controlled by thermostat. Within one day after hatching, the most photopositive and active larvae were selected, and then used for experiments. A 5-ml glass pipette was used to retrieve active larvae from the rearing container (mass culture) and to place them into the one-liter plastic test container containing the test solutions (20 individuals per container). Half of the aerated test water in each container was replaced daily. The larval stage was identified based on the setal number on maxillipedal exopods, under a binocular stereomicroscope.

Newly hatched nauplii of *Artemia* sp. were added daily to each bowl as larval food. In addition, finely chopped meat of the short-necked clam *(Ruditapes philippinarum)* was fed to megalopa. Moulting, survival and development duration were checked for each larval stage daily between 7:00 am and 7:00 pm. Dead larvae were preserved in 50% ethylene glycol solution for later re-identification of stages. Experiments were terminated when all the larvae had moulted to the first crab stage or died. Development duration for larvae at each salinity level was analyzed using a two factor analysis of variance (ANOVA) on the statistical package Minitab 11.12 for Windows.

Results

Larval survival of *N. trispinosum* from hatching through first crab stage occurred over the range of tested salinities (15-35‰), with a slight tendency of higher survival in 25‰ at 25°C, 20‰ at 30°C and 30‰ at 20°C (Table 1). However, 0-10‰ appeared unsuitable, 100% mortality occurring after 12-18 hours exposure. At the time of metamorphosis from the fifth zoea to the megalopa stage, survival was higher in 25‰ at 30°C, 25‰ at 25°C and 30‰ at 20°C than at 15‰ or in full-strength seawater (35 ‰) (Table 1). At 20, 25 and 30°C, development was successful in the salinity ranges were tested (Table 1), but with different survival and different development duration. Development duration are almost similar except for the first zoea at 20°C and fifth zoea at 30°C. Significant differences ($P<0.05$, <0.01) among the development duration of larvae at different salinity levels tested at different temperature conditions was observed (Table 2).

Total development duration required for metamorphosis from first zoea to first crab stage at five different salinities ranged from 28-32 days at 20°C, 24-29 days at 25°C and 25-30 days at 30°C (Fig. 1). Average development duration was 30 days at 20°C, and 27 days at 25 and 30°C in all tested salinities (15-35‰). However, minimum duration recorded 24 days at 25‰ (25°C), 25 days at 20-25‰ (30°C) and 28 days at 25‰ (20°C). Results show that reduced salinity (15‰) or full-strength seawater (35‰) increased development duration significantly when compared with intermediate salinity (20-25‰). Significant differences ($P<0.01$) in the total duration for complete larval development at different salinity levels tested at different temperature conditions was observed (Fig. 1).

Table 1. Development duration and survival rate of *Neosarmatium trispinosum* from hatching to first crab reared under five different salinity conditions at three constant temperatures. Salinity 0, 5 and 10‰ are not included, since no larvae survived these treatments within 12-18 hours after exposure. Number of live individuals is provided in parenthesis. Z = zoea, M = megalopa

Stages	Temp.	15‰		20‰		25‰		30‰		35‰	
	(℃)	*S (%)*	*D (day)*	*S (%)*	*D (day)*	*S (%)*	*D (day)*	*S (%)*	*D (day)*	*S (%)*	*D (day)*
Z-I	20	65.0 (13)	5.0±0.46	80.0 (16)	5.0±0.37	90.0 (18)	4.0±0.34	100.0 (20)	5.0±0.32	85.0 (17)	5.0±0.35
Z-II	20	92.3 (12)	5.0±0.30	81.3 (13)	4.0±0.29	88.9 (16)	4.0±0.26	95.0 (19)	4.0±0.33	88.2 (15)	5.0±0.27
Z-III	20	83.3 (10)	5.0±0.41	84.6 (11)	4.0±0.15	87.5 (14)	4.0±0.28	89.5 (17)	4.0±0.35	66.7 (10)	5.0±0.33
Z-IV	20	80.0 (8)	4.0±0.32	90.9 (10)	4.0±0.33	78.6 (11)	4.0±0.45	88.2 (15)	4.0±0.38	80.0 (8)	4.0±0.27
Z-V	20	62.5 (5)	4.0±0.32	60.0 (6)	5.0±0.29	72.7 (8)	5.0±0.38	86.7 (13)	4.0±0.29	75.0 (6)	4.0±0.29
M	20	20.0 (1)	9.0±0.00	33.3 (2)	8.0±0.00	37.5 (3)	7.0±0.00	61.5 (8)	8.0±0.38	50.0 (3)	8.0±0.35
Z-I	25	80.0 (16)	5.0±0.37	100.0 (20)	4.0±0.32	100.0 (20)	4.0±0.32	100.0 (20)	4.0±0.32	95.0 (19)	5.0±0.33
Z-II	25	81.3 (13)	5.0±0.29	95.0 (19)	4.0±0.33	100.0 (20)	4.0±0.32	85.0 (17)	4.0±0.25	84.2 (16)	4.0±0.26
Z-III	25	84.6 (11)	4.0±0.32	84.2 (16)	4.0±0.26	95.0 (19)	3.0±0.24	82.4 (14)	4.0±0.28	81.3 (13)	4.0±0.29
Z-IV	25	72.7 (8)	4.0±0.35	81.3 (13)	4.0±0.29	100.0 (19)	4.0±0.33	85.7 (12)	4.0±0.21	84.6 (11)	4.0±0.32
Z-V	25	25.0 (2)	4.0±0.00	84.6 (11)	4.0±0.32	94.7 (18)	4.0±0.24	83.3 (10)	4.0±0.33	72.7 (8)	4.0±0.25
M	25	50.0 (1)	7.0±0.00	9.1 (1)	7.0±0.00	55.6 (10)	5.0±0.33	30.0 (3)	6.0±0.41	25.0 (2)	8.0±0.00
Z-I	30	80.0 (16)	4.0±0.37	100.0 (20)	4.0±0.28	100.0 (20)	4.0±0.32	95.0 (19)	4.0±0.17	65.0 (13)	5.0±0.35
Z-II	30	93.8 (15)	4.0±0.27	100.0 (20)	4.0±0.32	95.0 (19)	4.0±0.33	94.7 (18)	4.0±0.30	76.9 (10)	4.0±0.41
Z-III	30	86.7 (13)	3.0±0.29	95.0 (19)	4.0±0.29	89.5 (17)	4.0±0.31	88.9 (16)	4.0±0.37	70.0 (7)	4.0±0.38
Z-IV	30	84.6 (11)	4.0±0.39	100.0 (19)	3.0±0.24	88.2 (15)	4.0±0.38	87.5 (14)	4.0±0.34	71.4 (5)	4.0±0.00
Z-V	30	90.9 (10)	4.0±0.41	89.5 (17)	3.0±0.31	80.0 (12)	3.0±0.00	78.6 (11)	3.0±0.22	60.0 (3)	4.0±0.00
M	30	40.0 (4)	9.0±0.35	76.5 (13)	7.0±0.29	83.3 (10)	6.0±0.33	27.3 (3)	8.0±0.00	33.3 (1)	9.0±0.00

Table 2. Comparison of larval development duration of *Neosarmatium trispinosum* at different salinity and temperature levels
Z = zoea, M = megalopa, NS = not significant

Source	*DF*	*F–value*						*P–value*					
		Z-I	Z-II	Z-III	Z-IV	Z-V	M	Z-I	Z-II	Z-III	Z-IV	Z-V	M
Salinity	4	20.745	12.834	4.564	3.429	4.000	70.940	<0.01	<0.05	NS	NS	NS	<0.01
Temperature	2	22.340	9.626	89.480	3.429	76.000	73.504	<0.05	NS	<0.05	NS	<0.05	<0.05
Sal. x Temp.	8	6.383	5.615	11.268	3.429	16.000	9.402	<0.01	<0.01	<0.01	<0.05	<0.01	<0.01

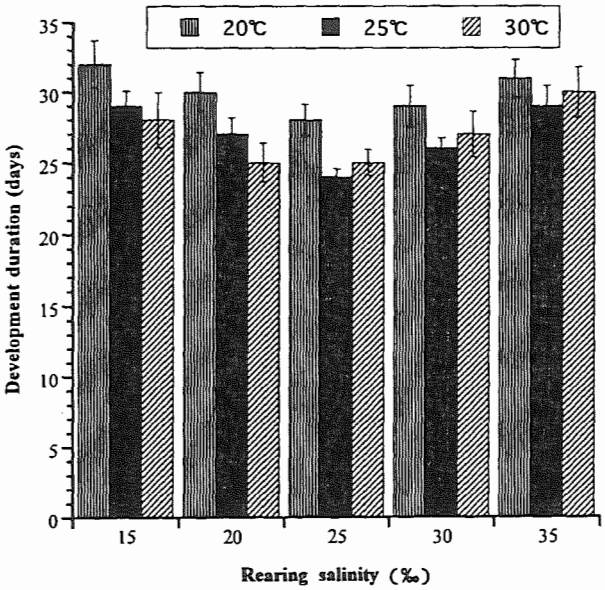

Fig. 1. Development duration to the first crab stage of *Neosarmatium trispinosum* under five different salinity conditions at three constant temperatures. Vertical bars indicate standard deviation. Significant differences 9P<0.01) were found among the salinity levels tested.

Discussion

The larvae of laboratory reared *N. trispinosum* were able to develop successfully through metamorphosis in a wide range of salinities. Compared with the previous observations on its congener *N. indicum* (Islam *et al.* 2002a), however, the larvae in the present study showed a less euryhaline response. A salinity of 20-25‰ at 25-30^{0}C represents a suitable condition for early larval stages and possibly for the megalopa. Hence, the intermediate salinity (20-25‰ at 25-30^{0}C) appears optimum for the larval development of *N. trispinosum.*

At 15‰, *N. trispinosum* larvae had poor survival and delayed development, while Islam *et* al. (2002a) reported for this condition a low mortality and occasionally some survival even at 5 or 10 ‰ in *N. indicum.* Compared with the optimum condition (20- mortality was higher at 15 and 35‰, with an increasing development duration. Development to the first crab stage was completed, with different percentages, at salinities ranging from 15-35‰. This represents a narrow range than in other sesarmid crabs as *Sesarma curacaoense* (Schuh and Diesel 1995a), *Armases miersii* (Schuh and Diesel 1995b), *Perisesarma bidens* (Islam *et al.* 2000) and *N. indicum* (Islam *et al.* 2002a).

Development to the first crab stage in *A. cinereum* was successful at 20.1 and 26.7 ‰ but not at 12.5 and 31 ‰ (Costlow *et al.* 1960) and individuals of *A. ricordi* survived at 15-35‰, but died at 10‰ or lower salinities (Diesel and Schuh 1998), which was similar to the present results. Unfortunately, the above authors and the present study did not test at higher salinities, so that the upper limit of salinity tolerance during the early

development of *A. cinereum, A. ricordi* and *N.* trispinosum remain unknown. In all these species including the present one, the first zoea most probably hatches at low salinity near shore or estuarine waters; subsequent zoeal stages occur in the marine environment, and waters of lower salinities are invaded by the megalopa (Costlow *et al.* 1960, Alvarez and Ewald 1990).

Tolerance of *N.* trispinosum larvae to low salinity decreases in successive stages. The first zoea had high survival rates at 20-30‰, and developed well at 25‰ with a slightly shorter duration. This may reflect an adaptation of the first zoea to regular release in brackishwater and early development in marine water habitats. Laboratory investigation showed that the later zoeal stages of *N.* trispinosum exhibit a slight preference for brackish to marine conditions, where they showed the shortest development and highest survival rates. At 15 and 35‰, they displayed clearly delayed development and increased mortality. This shows that *N. trispinosum* is a species whose development takes place in near shore water.

Results of the present studies revealed that the major part of the larval development of *N. trispinosum* appears to take place in lower estuaries and in coastal oceanic waters, where salinities between ca 20 and 30‰ are found. This salinity range was also found to be optimum for larval development in other brackishwater sesarmid species (Costlow *et al.* 1960, Anger *et al.* 1990, Islam *et al.* 2000, 2002a). The salinity tolerance of other sesarmid larvae decreased during development where the first zoea are released into brackish near shore waters, and subsequent stages occur in the relatively stable conditions in lower estuaries (Schuh and Diesel 1995a,b, Diesel and Schuh 1998, Islam *et al.* 2000, 2002a).

The osmoregulation in decapod crustaceans did not change during development from larval hatching through the adult phase (Charmantier *et al.* 1998, Charmantier and Anger 1999). Successful development of *Sesarma curacaoense* from hatching to the end of the first crab stage through metamorphosis occurred in the full salinity range tested (15-32‰), although mortality was significantly enhanced and development delayed at 15‰ (Anger and Charmantier 2000). Our results are most similar with these findings. Larval survival of *A. miersii* was frequently higher at 15-25‰ than in seawater (Anger 1996), while higher mortality occurred at the extremes of 10 and 55‰. The present result is again similar to those observed in *A. miersii.* Lowest mortality and shortest development duration occurred generally at 15-25‰, indicating an optimum at moderately reduced salinities (Anger *et al.* 2000). The optimal salinity required for complete development of each larval stage of *N. trispinosum* varied at ca. 20-30‰. The salinity of the Shimajiri mangrove swamp is nearly 20-25‰, which is lower than seawater and similar to the rearing water. Hence, the present results suggest that the larvae of *N. trispinosum* develop in estuarine water and recruit to the mangrove swamp at the megalopa stage, where they spend the rest of their lives.

Temperature had a strong effect on development duration in *A. miersii* (Schuh and Diesel 1995b). Larvae of *N. trispinosum* reared at 20°C took a longer period to reach the first crab stage than those reared at 25 or 30°C, and they suffered higher mortality at lower salinities. Similar effects have been reported for other sesarmid species reared

under comparable constant laboratory conditions (Costlow *et al.* 1960, Alvarez and Ewald 1990, Schuh and Diesel 1995b). The development duration of *N. trispinosum* at 25°C was intermediate between those observed at 20°C and 30°C, and survival was higher. The results are similar to those of *A. miersii* (Schuh and Diesel 1995b). The conditions of constant temperature and salinity used in this study are obviously not found in the larvae's natural environment, but the ecological significance of our results can be appreciated when the situation in the larval habitat is considered.

In future studies, larvae should be reared under optimum salinity conditions to the megalopa stage and then transferred to different conditions of gradually decreasing salinity. Those tests combined with field conditions, would hopefully show at which developmental stages return from the sea to brackish or estuarine water, and eventually, to freshwater habitats, and where their metamorphosis takes place (Anger *et al.* 1990). Once the complete life cycle is known, this species could become an interesting and suitable model for the studies of larval development in mangrove sesarmid crabs and hence, a model for the development of physiological adaptations in crustacea during the transition from life in the sea to freshwater and terrestrial environments.

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