



EFFECTS OF TEMPERATURE AND SALINITY ON THE OVARIAN CYCLE AND THE EMBRYONIC DEVELOPMENT OF THE INVASIVE SHRIMP *PALAEEMON MACRODACTYLUS*

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A B S T R A C T

The oriental shrimp *Palaemon macrodactylus* Rathbun, 1902 was detected first in Argentina in 2000 in a fully marine environment (Mar del Plata) and more recently, in two estuarine areas. Here we examined combined effects of four salinities (1, 5, 12, 23, 34 psu) and two temperatures (20°, 25°C) on survival, reproductive cycle of females and embryonic development in shrimps from the marine population of Argentina. Survival was higher than 80% in all the treatments; however, at the lowest salinity (1 psu), all females died after 12 days irrespectively of the temperature condition. Most shrimps (>80%) developed their ovaries and produced eggs at all salinity-temperature tested combinations, but all females lost their eggs after 2 days at 5 psu; a complete embryonic development occurred only at 12 and 34 psu. At the lowest temperature, the ovarian development was delayed in different proportions for individual levels of salinity. Therefore, *P. macrodactylus* from Mar del Plata harbor survived and completed all reproductive events at salinities ≥ 5 psu, but embryonic development was only successful at salinities ≥ 12 psu. Our results indicate that this non-native species is capable of invading estuarine habitats over the Argentinean coast but not oligohaline or freshwater environments.

KEY WORDS: brackish water, invasive species, *Palaemon macrodactylus*, reproduction, salinity and temperature tolerance

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I N T R O D U C T I O N

The oriental shrimp *Palaemon macrodactylus* Rathbun, 1902 is native from the NW Pacific Ocean coast (Japan, Korea and north of China) (Rathbun, 1902). In the last 50 years, this species has been recorded out of its natural range of distribution associated mainly to estuaries along coastal areas in the Pacific Ocean, on the US west coast (Newman, 1963; Jensen, 1995) and in South Australia (Buckworth, 1979). In North-Atlantic waters it has invaded the western coast of Europe extensively (Ashelby et al., 2004; Cuesta et al., 2004; d'Udekem d'Acoz et al., 2005; González-Ortegón and Cuesta, 2006; Béguer et al., 2007; Chicharo et al., 2009; Lavesque et al., 2010), the Black Sea (Micu and Niță, 2009; Raycov et al., 2010) and the US east coast (New York and Connecticut estuarine areas) (Warkentine and Rachlin, 2010). In the southwest coast of South America this shrimp species was first detected at Mar del Plata harbor (38°03'S, 57°31'W; Argentina) in 2000, likely introduced from the Pacific with discharged ballast water (Spivak et al., 2006). A stable population is now established in this fully marine environment (Vázquez et al., 2012), where no other caridean shrimp species occurs with the exception of the native alpheid *Betaeus lilianae* Boschi, 1966 in very low numbers.

The harbor of Mar del Plata has been considered a potential centre of dispersion of *P. macrodactylus* towards nearby estuarine environments (Spivak et al., 2006), as it was observed to happen in another invasive crustacean with planktonic larvae, *Balanus glandula* Darwin, 1854, which arrived to Mar del Plata harbor in the early 1970's and spread immediately northward and southward. Recently, three new records of *P. macrodactylus* have been reported in Argentina, Bahía Samborombón (36°19'S, 57°25'W), Bahía Blanca (38°44'S, 62°22'W), and Río Negro (41°1'S, 62°47'W) (Martorelli et al., 2012), all of them typical estuarine environments.

This species is able to complete their entire life cycle inside estuaries such as Guadalquivir in Spain and Gironde in France (González-Ortegón and Cuesta, 2006; Béguer et al., 2011). The knowledge of factors facilitating or limiting the establishment of non-native macroinvertebrate species may help to predict future species replacements and to derive management options for invasive species (Verbrugge et al., 2011). Although most investigations have focused on salinity tolerance of *P. macrodactylus* adults (Born, 1968; González-Ortegón and Cuesta, 2006), nothing is still known about the effects of salinity (and temperature) on the reproductive performance of this species.

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The present study examines the hypothesis that the oriental shrimp, *P. macrodactylus*, is able to survive, reproduce and develop in a wide range of salinity-temperature combinations. If this hypothesis is correct, then: 1) females belonging to the marine population of Mar del Plata harbor should survive and reproduce in both sea water and reduced salinities 2) embryonic development should occur in both conditions, and 3) there should be a salinity optimum in which the time necessary to complete ovary maturing and embryogenesis were shorten, which may be affected by temperature.

These predictions were tested under controlled experimental conditions analyzing the effects of five salinities (1, 5, 12, 23 and 34 psu) and two temperatures (20 and 25°C) on female survival and on time necessary to complete the ovarian cycle as well as the embryonic development, in shrimps from the fully marine population living at Mar del Plata harbor (Argentina).

MATERIALS AND METHODS

Shrimp Collection

Females (average CL 9.06 ± 1.17 mm) with fully developed ovaries (occupying at least three quarters of the cephalothoracic dorsal surface, colour dark green or brown, directly observed throughout dorsal carapace) (Ituarte et al., 2010) and mature males (average CL 6.1 ± 0.85 mm; with appendix masculina in the second pair of pleopods) were collected in January 2008 and 2009 from Mar del Plata harbor ($38^{\circ}03'S$, $57^{\circ}31'W$), with a hand net, 300 μ m mesh. The sampling site is located in an area used for sailing activities; shrimps were collected from the piles of the marinas.

Experimental Procedures

In the laboratory, females were kept isolated in individual plastic containers (500 ml) with aerated sea water at 20°C and 12:12 L:D cycle until they spawned. Since females were not fertilized by males, eggs were released to the bottom of the aquaria during the next day. Immediately, the females with empty ovaries were assigned to one of the following combinations of four salinities (1, 5, 12, and 34 psu) and two temperatures (20 and 25°C). An extra salinity (23 psu) was tested only at 20°C. Shrimp were transferred to each experimental salinity below 34 psu in progressive acclimation steps of 8 hours at 23, 12, and 5 psu (as corresponding). Every female was kept in individual plastic containers with small holes at sides and bottom to allow water circulation, immersed in bigger container with aerated water. A dark tube (25 mm diameter, 40 mm length) was provided to each female as refuge. A total of 9 females were placed together inside 5l aquaria with water of the proper salinity.

Each aquarium was an independent replicate for each salinity-temperature combination. Three replicates per salinity were maintained at 20°C and two at 25°C. Shrimps were fed daily with fish food (TetraMin Pro®; 12% lipids, 46% proteins) and fresh squid tentacles. Water was continually aerated and changed weekly.

Four stages of ovary maturation were determined based on *Palaemonetes pugio* Leach, 1814 staging (Bauer and Abdalla, 2000). Stage 1 or "empty ovaries": females with newly laid eggs and without evidence of ovarian development; Stage 2: ovaries pale grey, filled with oöcytes; stage 3: ovaries brown or green, filled with oöcytes; ovarian filaments larger, occupying the space between the anterior and the posterior part of the cephalothorax; stage 4: fully developed ovaries filling most of the cephalothorax and the first pleomere, females ready to spawn eggs. All females suffered a parturial molt, i.e., a molt immediately previous to egg laying (Bauer and Abdalla, 2000). Other recorded molts not related to egg laying were considered non-parturial molts.

Just before finishing the development of ovaries, a male was added to each female container to allow fertilization of eggs. Females often eat males, in which cases replacements were provided. Shrimps were checked daily to record events of death, ovarian condition, molting, spawning, egg loss, or larval hatching. Dead shrimps were immediately removed from the aquaria. The following variables were registered:

1) Percentage of i) survival (final number \times 100/initial number); ii) females that completed the gonad maturation (number of females with

stage 4 ovaries \times 100/survival number); iii) females with and without molt before gonad maturation (number of females that had or had not molted before gonad maturation \times 100/number of females with mature gonads); iv) fertilized females (number of females laying fertilized eggs \times 100/number of females with mature gonads).

2) Period (in days) between i) first egg spawning or non parturial molt, and second egg spawning (period of gonad development); ii) second egg spawning and larval hatching (period of embryonic development).

Statistical Analysis

Since the treatment at 23 psu was carried out only at 20°C, it was not considered in multiple comparisons (effects of salinity-temperature combinations), but it was separately compared with the other salinity treatments at 20°C.

Survival curves were compared between salinities within each temperature treatment and among all female groups at each temperature-salinity combination using a nonparametric LogRank test (SigmaStat for Windows, Version 3.5). It provides a chi-square statistic, assuming that all survival time data are equally accurate and all data will be equally weighted in the analysis. When LongRank test indicated significant differences among groups, they were tested *a posteriori* with the Holm-Sidak test. Since some females went through an extra molt (EM) before starting ovarian maturation, whereas others did not (NEM) (see results and Fig. 2), the effect of salinity and temperature on the proportion of EM females was evaluated with a Chi-square test, using the observed frequencies a) at each temperature-salinity combination (interaction); b) at each temperature treatment; c) at each salinity treatment. Yates correction was applied if necessary. Ovarian maturation period was compared between EM and NEM females by a Student *t*-test within each salinity-temperature treatment. Differences in ovarian development period were evaluated with two-way ANOVA with unequal replication, with salinity (5, 12, and 34 psu) and temperature (20 and 25°C) as factors (Zar, 2010). Embryonic developmental period was analyzed with two-way ANOVA with salinity (12 and 34 psu, see below) and temperature (20 and 25°C) as factors.

An additional one-way ANOVA test was used to compare 23 psu treatment with the other salinities at 20°C.

All ANOVAs were performed after checking for normality and equality of variance (Kolmogorov-Smirnov and Cochran test, respectively; Underwood, 1997). When ANOVA indicated differences between treatments, they were tested *a posteriori* with the Honestly Significant Differences (HSD) test for different sampling size.

RESULTS

Survival

At the lowest salinity treatment (1 psu) all females died during the first 12 days of experimentation irrespective of temperature; thus they were not considered in the survival analysis. By contrast, more than 80% of the females survived until the end of the experiment in all the remaining treatments (Table 1). Mortality rates did not differ among salinities when they were analyzed separately for each temperature (20°C: $\chi^2 = 2.76$, $df = 3$, $P = 0.43$; 25°C: $\chi^2 = 1.98$, $df = 2$, $P = 0.37$). Death took place always during the first week of the study. After an observation period of 2 months, average final survival was 95.28 ± 3.65 and $84.17 \pm 3.71\%$ in 20 and 25°C, respectively. Mortality rates differed when all female groups and all salinity-temperature combinations were tested together ($\chi^2 = 15.82$, $df = 6$, $P = 0.015$) due to differences between the two groups of females with the highest (100%; 20°C-23 psu) and the lowest (80.95%; 25°C-12 psu) survival percentages (Holm-Sidak: $P = 0.001$).

Ovarian Maturation

All females collected from the field and individually kept (without a male) went through a parturial (spawning) molt before becoming ovigerous ("empty ovaries"; ovarian stage 1) at the beginning of the experiments. Between 78 and 100%

Table 1. *Palaemon macrodactylus*. Survival of females (% and total number of each at the beginning, between parenthesis) at the end of the experiment for each temperature-salinity combination.

T (°C)	Salinity values (psu)				
	1	5	12	23	34
20	0	96.15 (26)	91.66 (36)	100 (32)	93.33 (30)
25	0	83.33 (18)	80.95 (21)	–	88.23 (17)

of the shrimps were able to reach the ovarian stage 4 under all experimental conditions, except 1 psu salinity (Fig. 1). Ovarian maturation started just after the parturial molt in most shrimps (80.3%), without any other extra molting event during their ovarian development. This group was called non-extra molt (NEM) females (Fig. 2a). The remaining 19.7% had an extra molt before their ovaries started to mature and were called extra molt (EM) females (Fig. 2b); in these females ovaries remained without any observable change, either in form or color, until the extra molt. In both cases, a parturial molt took place prior to the next spawn (Fig. 2). The existence of an extra molt was very variable among replicates at each salinity-temperature combination (Table 2). Nevertheless, the proportion of EM females was not related to temperature ($\chi^2 = 0.825$; $df = 1$; $P = 0.364$) but depended on salinity, being higher at 5 psu ($\chi^2 = 12.10$; $df = 2$; $P = 0.002$) and no temperature-salinity interaction existed ($\chi^2 = 0.169$; $df = 2$; $P = 0.91$).

Time to complete ovarian maturation at each temperature salinity combination did not differ between NEM and EM (Student test, all $P > 0.05$), except in the 25°C-5 psu treatment, in which ovarian development was 6 days longer in EM females (Student test, $P = 0.024$). For that reason, EM and NEM females were pooled for each treatment except in 25°C-5 psu, where only the most numerous group (65% NEM females) were selected to compare the effect of salinity and temperature over the duration of ovarian development.

The duration of ovarian development was affected by temperature and salinity, and there was interaction between these factors (Table 3, Fig. 3). The ovarian development was longer at 20°C than at 25°C but the difference varied among salinities: it was 32% at 5 psu, 24.7% at 34 psu and 21.6% at 12 psu (Fig. 3).

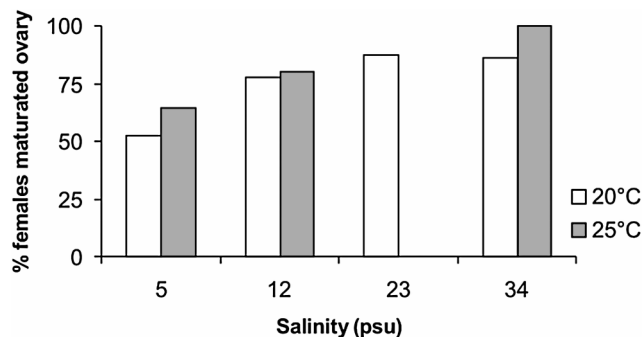


Fig. 1. *Palaemon macrodactylus*. Percentage of females that matured their ovary at two temperatures (20 and 25°C) and four salinities (5, 12, 23 and 34 psu). Females maintained in 1 psu did not survive.

Embryonic Development

Most shrimps were able to develop their ovaries and spawn, although some of them were incapable of retaining their eggs (Table 4). At the lowest salinity (5 psu), all females lost their eggs after 2 or 3 days irrespective of the temperature. The remaining salinities had no effect on the success of brooding ($\chi^2 = 1.088$; $df = 1$; $P = 0.297$), but temperature had ($\chi^2 = 15.235$; $df = 1$; $P < 0.001$); more than 70% of the females incubated their embryos successfully at 25°C, whereas a maximum of 36% succeeded at 20°C (Table 4). No interaction existed between temperature and salinities ($\chi^2 = 0.488$; $df = 1$; $P = 0.481$).

The time to complete embryonic development was lengthened at the lower temperature and there was an interaction between temperature and salinity (Table 5). The development at 20°C was longer at 34 than 12 psu (7 and 2 days longer respectively) (Fig. 4) while there were no differences among salinities at 25°C. The ANOVA performed to compare 23 psu with the remaining salinities at 20°C showed significant differences ($P < 0.001$), the time to complete embryonic development was shorter at 34 psu than at the lower salinities (HSD, $P < 0.001$), and no differences existed between 12 and 23 psu (HSD, $P = 0.89$).

Ovarian Re-maturation

At the end of the experiments, the ovaries of 42 of the 43 females that incubated embryos were in stages 3 or 4 (mature) and the remaining female had a stage 2 ovary. Unlike what was observed at the beginning of the experiment, shrimps did not go throughout an extra molt before maturing their ovaries again.

DISCUSSION

In most decapod crustaceans, reproduction is strongly influenced by environmental factors, and it commonly occurs in a narrower range of conditions than that necessary for survival and growth (Sastry, 1983). The ability of a potential invasive species to reproduce in different environmental conditions may thus result in a crucial step during the invasion process. Temperature and salinity are the most studied factors affecting reproduction in decapods, acting alone or in combination with other factors as shelter, substrate, light cycle or food conditions (Gelin et al., 2001; Lee, 2003; Ituarte et al., 2010). Our experimental data demonstrate that the range of salinities for successful reproduction and embryonic development of *P. macrodactylus* (12-34 psu) was narrower than the range of salinities for adult survival (5-34 psu), regardless of the temperature.

Adults, postlarvae and a few larvae of *P. macrodactylus* were found at salinities below 5 psu (González-Ortegón et al., 2006; Béguer et al., 2011). Moreover, adults are able to osmoregulate at 2 psu at least during several days (Born, 1968; González-Ortegón et al., 2006). Nevertheless, in our experiment, all females died after 12 days at the lowest salinity treatment (1 psu) but survived and mature their ovaries at 5 psu, although their embryos were incapable of developing at this salinity. The Mar del Plata harbor population lives in a fully marine environment without freshwater supply, which differs from most other populations living in estuaries or brackish-water habitats. In consequence, the tolerance

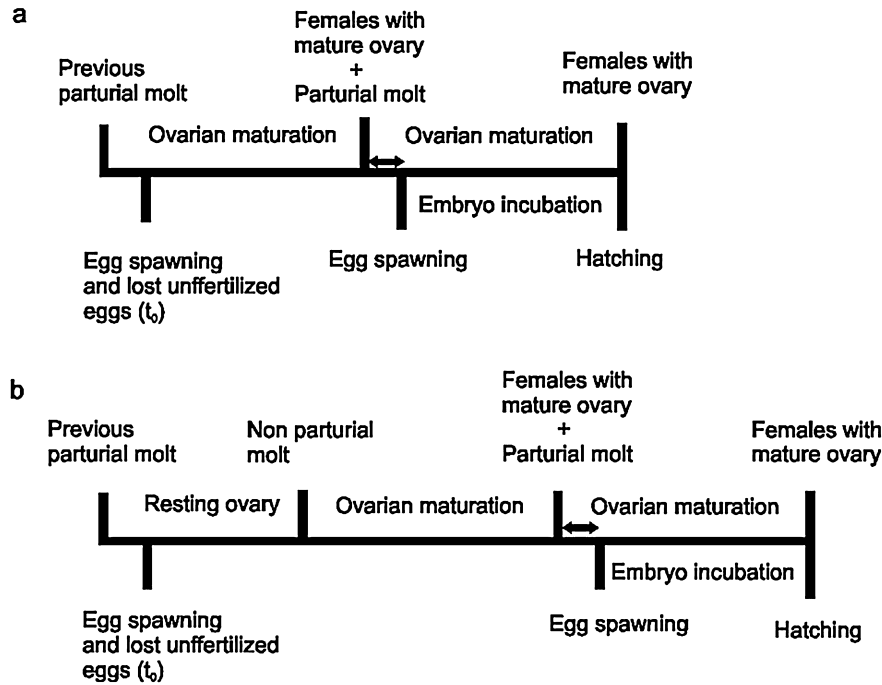


Fig. 2. *Palaemon macrodactylus*. Schedule of egg development when a) gonadal maturation occurred immediately after a parturial molt (NEM) b) gonadal maturation after a resting period (EM). t_0 : beginning of the experiment. Double arrow indicates the period in which fertilization occurred.

Table 2. *Palaemon macrodactylus*. Percentage of females with matured ovaries after a non parturial extra molt (EM females) for each temperature-salinity combination except 1 psu (no survival). In parenthesis: total number of females for each combination.

T ($^{\circ}\text{C}$)	Salinity values (psu)			
	5	12	23	34
20	45 (20)	22.22 (27)	13.33 (30)	13.63 (22)
25	35.71 (14)	6.6 (15)	–	0 (14)

Table 3. *Palaemon macrodactylus*. Two-way ANOVA for duration of ovarian maturation at two temperatures (20 and 25 $^{\circ}\text{C}$) and three salinities (5, 12 and 34 psu). MS, mean squares; F , test statistic; P , probability of error.

Source of variation	df	MS	F	P
Temperature	1	576.95	125.447	<0.0001
Salinity	2	122.57	26.65	<0.0001
Temperature * Salinity	2	16.98	3.69	0.028
Error	98	4.60		

range of individuals living permanently in low-salinity waters could differ, as a result of the acclimation to that condition. On the other hand, great differences among populations are not expected considering that the invasion is recent (no more than 15 years).

Most females that survived in all temperature-salinity combinations developed their ovaries and spawned eggs. Nevertheless, many of them showed a period of arrested development before starting gonad maturation, more frequent at the lowest salinity tested (5 psu). In addition, females that had an extra molt event before starting their ovary maturation at 5 psu did not experiment an acceleration of the

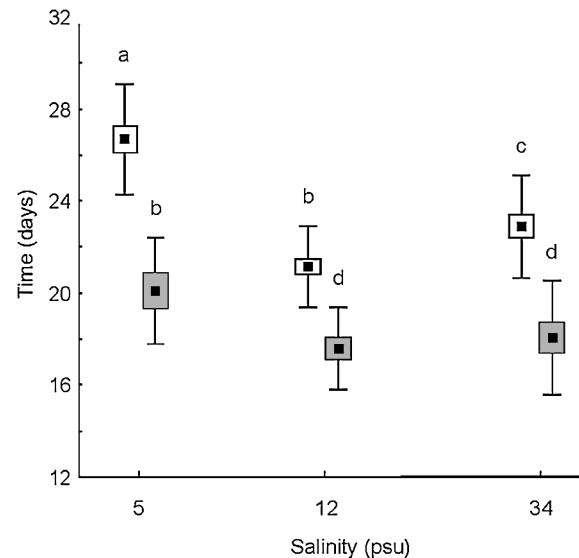


Fig. 3. *Palaemon macrodactylus*. Time (in days) to complete gonad maturation in females cultured in the combination of two temperatures (20, 25 $^{\circ}\text{C}$, grey boxes) and three salinities (5, 12 and 34 psu). Mean value (black squares), standard error (boxes) and standard deviations (vertical lines) are shown. Different letters indicate significant differences between temperatures and salinities.

Table 4. *Palaemon macrodactylus*. Percentage of females that kepted their clutch of eggs for each temperature-salinity combination.

T ($^{\circ}\text{C}$)	Salinity value (psu)		
	12	23	34
20	14.8	33.3	36.3
25	73.3	–	71.4

Table 5. *Palaemon macrodactylus*. Two-way ANOVA for duration of embryonic development between temperatures (20 and 25°C) and salinities (12 and 34 psu). MS, mean squares; *F*, test statistic; *P*, probability of error.

Source of variation	df	MS	<i>F</i>	<i>P</i>
Temperature	1	124.95	235.16	<0.0001
Salinity	1	20.53	38.65	<0.0001
Temperature * Salinity	1	37.24	70.09	<0.0001
Error	29	0.53		

ovarian cycle at 25°C compared to 20°C, as occurred in the remaining females in other salinity conditions. If we consider the presence of an extra molt as an evidence of stress, the higher incidence of this event at the lowest salinity may be considered the result of an additional stressing factor for females maturing their gonads, which affects not only the time to start maturation but the minimum time lapse to finish it. At the end of the experiments, however, females from all the experimental conditions had re-matured their ovaries without an extra molt, indicating perhaps an acclimation to low salinity and captivity. This suggests that a longer period of acclimation to captivity before start the experiments and longer and more gradual acclimation to low salinities could diminish the occurrence of extra, non-parturial molts. The optimum values of salinity for ovarian development (minimum time) appears to occur at intermediate values (12 psu) in this species when combined with the lowest temperature (20°C), and it is equally good in intermediate or marine conditions (34 psu) when temperature is high (25°C). In addition to the higher proportion of females with a delayed ovarian development at 5 psu, all females lost their embryos after 2 days at this salinity suggesting a massive mortality of embryos and/or a failure in fertilization or egg attachment.

Not only the period of ovarian maturation but also the embryonic development, was shorter in 25 than in 20°C. Accelerated ovarian cycle and embryonic development have been also related to higher temperatures in ectotherms in general

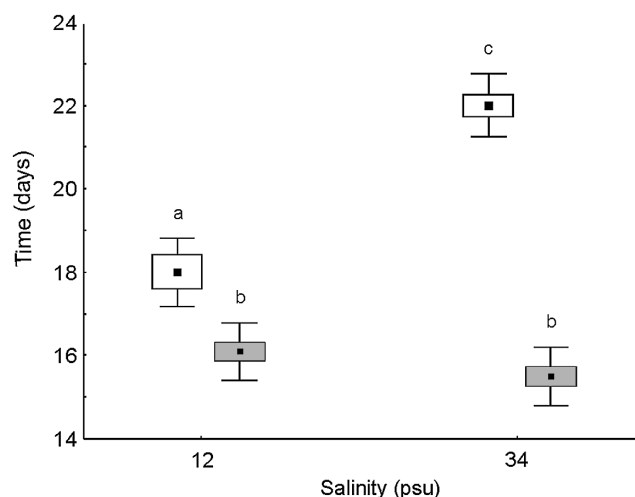


Fig. 4. *Palaemon macrodactylus*. Time (in days) to complete the embryonic development (from egg spawning to hatching) in two temperatures (20°C, white boxes and 25°C, grey boxes) and two salinities (12 and 34 psu). Mean value (black squares), standard error (boxes) and standard deviations (vertical lines) are shown. Different letters indicate significant differences between temperatures and salinities.

and crustaceans in particular, due to the effect of temperature over general metabolism (Carmona-Osalde et al., 2004; Brillon et al., 2005; Manush et al., 2006). In addition, the percentage of *P. macrodactylus* females capable of incubate their embryos was higher in the higher temperature, indicating a better performance of the ovigerous females at that condition. The optimum salinity for embryonic development at 20°C was the intermediate while at the highest temperature it was equally short in 12 or 34 psu as occurred with the ovarian development. Thus, the combination of 20°C with 34 psu, which is common in Mar del Plata harbor (Vázquez et al., 2012) and produced a lengthened embryonic development, indicates that the conditions for the reproduction and embryonic development in this recently invaded area are suboptimal for the species.

Although invasiveness cannot be predicted on the basis of a limited number of criteria, marine invasive species have a common ecological profile such as a wide range of salinity and temperature tolerance (Devin and Beisel, 2007). According to our results, the ability of *P. macrodactylus* to live and reproduce in a wide range of salinity and, at least, in the range of temperature tested, could be one of the keys of its success as invader. Two other characteristics of *P. macrodactylus* have been mentioned as probably improving their ability to invade new habitats. The first involves physiological characteristics; this species has an efficient metabolism and high tolerance to hypoxic conditions in brackish waters (González-Ortegón et al., 2009). The other, entails reproductive aspects, i.e., the co-existence of several cohorts differentiated by the combination of diverse values of reproductive effort, size at maturity, size specific fecundity and iteroparity (Omori and Chida, 1988a, b; González-Ortegón et al., 2009; Vázquez et al., 2012) which may allow to produce larvae for a long period, compensating possible failures in recruitment.

To sum up, survival and reproductive performance of *P. macrodactylus* females from Mar del Plata harbor are affected by low salinities, even though under mesohaline conditions (≥ 12 psu) reproduction and development were successful irrespective of temperature conditions. This shrimp species is unable to survive in salinities closer to freshwater conditions, and embryonic development was only possible at or above 12 psu. Our experimental data support the view that this population is able of invading new estuarine habitats over the Argentinean coast but at present the species has not been found in none of the brackish water environments existing close to Mar del Plata harbor (e.g., Mar Chiquita Lagoon and Quequén estuary, Vázquez, personal observation). Martorelli et al. (2012) suggested that the recent findings of *P. macrodactylus* in two new locations in the Argentinean coast represent northward and southward dispersions from Mar del Plata. Nevertheless, we consider such invasions more probable as new events coming from Europe or Asia, since both new sites are active harbors and are hundreds of kilometers far from Mar del Plata.

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