



Effects of temperature and salinity on larval survival and development in the invasive shrimp *Palaemon macrodactylus* (Caridea: Palaemonidae) along the reproductive season

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ABSTRACT

The invasive shrimp *Palaemon macrodactylus* is associated mainly with brackish waters. Previous studies raised the question if tolerance to low salinities differs between larvae and adults. To answer this question, the combined effects of two temperatures (20 and 25 °C) and four salinities (5, 12, 23 and 34 psu) on survival and development of larvae that hatched at the beginning, in the midpoint and near the end of a reproductive season (denoted early, middle season and late larvae respectively) were examined. The three types of larvae were able to survive and reach juvenile phase at salinities between 12 and 34 psu and at both temperatures. At 5 psu all larvae died, but 45% molted at least once. Temperature and salinity to a lesser extent, had effects on the duration of development and on the number of larval stages in all larval types. Development was longer at the lower temperature, especially in middle season and late larvae. Most early larvae reached the juvenile phase through 5 larval stages; the number of larval stages of middle season and late larvae was higher at 20 °C and in late larvae also low salinity produced extra stages. Low salinity (12 psu) and, in early and middle season larvae, low temperature produced lighter and smaller individuals. Response of larvae to environmental factors seems to be related in part to the previous conditions (maternal effects and/or embryo development conditions). The narrower salinity tolerance of larvae compared to adults and the ability of zoea I to survive at least some days at 5 psu may be related with an export larval strategy.

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1. Introduction

Most caridean shrimps (Crustacea, Decapoda, Caridea) live in the sea, although there are numerous estuarine and freshwater species, especially in families Atyidae and Palaemonidae. Many of these inland species have a shortened (less larval stages than marine counterparts; Bauer, 2004) or even direct development (Jalihal et al., 1993), but the extended ancestral condition has remained in others (Bauer, 2004; De Grave et al., 2008). The latter may exhibit life-cycle strategies ranging from export to retention of larvae in parental habitats. Export of larvae to adjacent waters, coastal or offshore marine, assures a more suitable environmental condition (Bauer, 2013). In fact, migration of berried females or recently hatched larvae to areas of intermediate or high salinities in the lower part of estuaries or to the sea have been documented either in freshwater or brackish water species (Cartaxana, 1994; Mc Dowall, 1992, 2007; Van den Brink and Van der Velde, 1986). On the other hand, adaptation of all life cycle stages to estuarine

conditions should include the development of osmoregulatory abilities in early ontogenetic stages (embryos and larvae), allowing for larval retention within the parental estuarine environment; this strategy is considered as a transitional stage in the evolution of limnic and terrestrial species (Strathmann, 1982).

Palaemon macrodactylus Rathbun (1902) is an invasive shrimp native from Japan, Korea and north of China (Rathbun, 1902). In recent decades, this shrimp has been recorded worldwide, and its current distribution includes the North and the South America, Australia and several European countries (see details in Ashelby et al., 2013). This species is generally associated to brackish environments, although purely marine populations have been found in Argentina (Spivak et al., 2006; Vázquez et al., 2012). The complete larval development of *P. macrodactylus* was described for the first time by Little (1969) and includes between 5 and 7 zoeal instars and a post-larva (= megalopa, see Anger, 2001). Little (1969) collected females of an introduced population at San Francisco Bay that inhabited brackish water but cultured their larvae successfully in seawater. Several aspects of *P. macrodactylus* adult biology have been studied: life history, reproduction, and tolerance of adults to different salinity, temperature and oxygen conditions

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(González-Ortegón et al., 2006; 2013; Lejeune et al., 2014; Omori and Chida, 1988; Vázquez et al., 2012, 2013a,b). High densities of adults and post-larvae (sic) have been recorded in European estuaries in salinities below 5 psu, although few larvae were found at those salinities (Béguer et al., 2011; González-Ortegón et al., 2010). Recently, several larval stages (zoeae III to VI), were collected in marine waters for the first time in the Western Mediterranean (Torres et al., 2012). All these information suggest that tolerance to diluted waters differs between larvae and juveniles or adults. In addition, it was proposed that *P. macrodactylus* is able to complete its life cycle in brackish water (González-Ortegón et al., 2006) but there is not information concerning the response of larval stages to different salinity conditions.

A dense population of *P. macrodactylus* lives in Mar del Plata harbor, Argentina (Vázquez et al., 2012, 2013a,b). This population showed a clear seasonal pattern of reproduction, settlement and growth and, particularly, three successive groups of reproductive females were distinguished along the reproductive season (Vázquez et al., 2012). A first group that included only the largest females was present at the beginning of the season (October–November). An intermediate size group appeared later (December–January); they reached maturity and began their reproductive activity although the largest females were still present. A third group of small females became evident near the end of the season (February–March); they grew and matured after large females died; this new group included all reproductive females at this moment. Females from each reproductive group produce eggs and larvae that differ in size and energy content (Vázquez et al., 2013b).

This paper raises the following questions: i) Are *P. macrodactylus* larvae able to survive and develop in the same range of conditions as adults? ii) Does temperature affect the ability of larvae to develop at different salinities? and iii) Since eggs and larvae from the successive female groups differed in size and energy content, do temperature and salinity equally affect larvae that hatched early, in the midpoint, and late in the reproductive season? To answer these questions, the effect of four salinities and two temperatures (representing estuarine conditions and usual temperatures during reproductive seasons in temperate habitats), on the survival, length of the larval phase, number of molts and juveniles size and weight was studied in larvae hatched from the three different groups of females present along the reproductive season.

2. Materials and methods

2.1. Shrimp collection

Ovigerous females with advanced embryos were collected at the beginning (November), in the midpoint (January) and near the end (February) of the reproductive season 2009–2010. Collections were made with a hand net, 300 μ m mesh, in an area used for sailing activities (Club Náutico) in Mar del Plata harbor (38° 03' S; 57° 31' W) where shrimps find refuges among fouling organisms that covered marina piles (see Vázquez et al., 2012). Females differed in size among periods; carapace length was 10.35 ± 0.39 mm at the beginning, 7.75 ± 0.31 mm in the midpoint and 5.58 ± 0.39 mm at the end of the reproductive season, respectively. Females, and the larvae they produced, from the beginning, midpoint and end of the reproductive season were denoted as early, middle season and late female or larvae, respectively. In the laboratory, females were individually cultured in transparent aquaria (200 ml) with aerated sea water at 20 °C, 34 psu, and 12:12 L:D cycle until larval hatching.

2.2. Experimental design

The experiment followed a factorial design with combinations of four salinities (5, 12, 23 and 34 psu), two temperatures (20 and 25 °C) and three times in the reproductive season (early, middle season and late larvae, collectively denoted “larval types”). In each combination of salinity, temperature and time in the reproductive season 10 larvae

from three different females (total 30 larvae) were used, excepting late females at 25 °C, where only larvae from two females were obtained (total 20 larvae). Larvae were cultured individually in plastic containers (25 ml), with 12:12 L:D cycle and fed daily with recently hatched *Artemia* sp. nauplii after water change. Larvae were transferred to experimental salinities below 34 psu in progressive acclimation steps of 8 h at 23, 12 and 5 psu (as corresponding).

Experiments started when larvae hatched and ended when all had reached juvenile phase or died. Every day, each larva was evaluated using a stereomicroscope to identify the developmental stage according to Little (1969). Individuals were considered juveniles when acquired a benthic behavior and when their antennae were more than three times the carapace length. Number of molts, time required to complete larval development and time and stage of death were registered. Larvae from three replicates were discarded because all of them died at the same day, few days after the beginning of the experiment: two from early larvae and one from middle season larvae, all reared at 25 °C/34 psu. Juveniles were frozen and then fixed in formalin 4%. Fixed specimens were measured (carapace length, CL) with an SZ40 Olympus stereo microscope furnished with a micrometric eyepiece, with an accuracy of 0.01 mm and their dry weight (DW) were determined with a microbalance (precision: 1 μ g).

2.3. Data analysis

Larval survival between treatments was compared using a Cox proportional hazards model (Cox and Oates, 1984). The Cox model can be used to test for differences among survival rates along the complete study rather than focusing at particular points in time. Treatment effects are analyzed by analysis of deviance, assessing the reduction in deviance due to the inclusion of each factor term using a Wald statistic. Statistical analyses were performed with version 3.1.2. of R software (R Core Team, 2014). We used the package “survival” to estimate model parameters and compare differences among treatments, and package “multcomp” to perform pairwise a posteriori multiple comparisons among survival coefficients.

Differences in developmental time from zoea I to juvenile phase, number of larval stages and juvenile size and weight were evaluated with General Linear Mixed Model (GLMM), with larval type (early, middle season and late), salinity (12, 23 and 34) and temperature (20 and 25 °C) as factors. Since larvae from different females were used each time, female identity was considered as a random factor nested within each larval type, to account for differences in larvae coming from different females. Variability in developmental time and number of stages of larval development within groups was lower than expected by Poisson distribution (data sub-dispersion). To account for this we used the function `glmmPQL()` in package “MASS”, of R software. For the analyses of larval size and weight a GLMM with a Gaussian distribution of the response variable was used (function `glmer()`, in the package “lme4”) and number of molts until reaching juvenile stage was considered as covariate to take into account the possible effect of the variation in the number of molts on the final size of larvae. Shapiro–Wilk’s and Levene’s tests were performed in all cases to check normality and homogeneity of variance respectively and data were transformed when necessary. Tukey’s HSD test was performed anytime significant differences appeared.

3. Results

Early, middle season and late larvae were able to survive and reach the juvenile stage at salinities between 12 and 34 psu at both tested temperatures. The analysis of survival curves (Fig. 1) showed significant differences among larval types ($X^2 = 13.22$, $P < 0.001$). The a posteriori test only showed differences between early and late larvae (Tukey’s test $P = 0.03$); early larvae have the highest and late larvae the lowest mortality. In addition, survival of each type of larvae was affected by

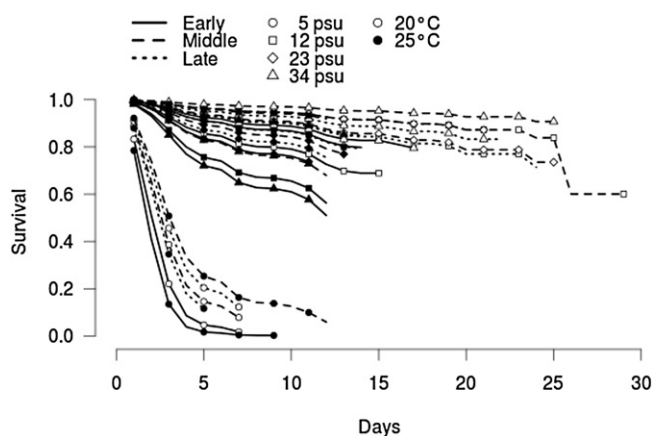


Fig. 1. *Palaemon macrodactylus*. Estimated survival curves from hatching to juvenile phase in larvae hatched at the beginning, midpoint and end of the reproductive season (early, middle season and late larvae) cultured at four salinities (5, 12, 23 and 34 psu) and two temperatures (20 °C and 25 °C).

the interaction between temperature and salinity ($\chi^2 = 8.92$, $P = 0.03$). All larvae died in 5 psu, independently of type and rearing temperature, differing significantly from the other treatments (Tukey's test, all $P < 0.05$; Fig. 1). In this condition, 81% of early larvae, 68% of middle season larvae and 47% of late larvae died as zoea I; the remaining larvae reached the stage of zoea II or III and only three middle season larvae reached the zoea V stage at 25 °C. Survival in all other conditions was high and no groups differed from each other (Tukey's test, all $P > 0.05$).

Time to complete larval development lasted between 9 and 25 days depending on larval type and rearing conditions; there were interactions between salinity and larval type and between temperature and larval type ($P < 0.001$ in both cases). Then, GLM was performed separately for each larval type to evaluate the effect of salinity and temperature on each one (Table 1). Development at 25 °C was similar in all larval types and data were pooled (11.28 ± 0.91 days) (Fig. 2a). Development at 20 °C differed among larval types and was significantly longer than at 25 °C (13.51 ± 1.16 , 20.15 ± 2.35 and 19.50 ± 2.23 days for early, middle season and late larvae respectively) (Fig. 2a). Salinity had effect in early and late larvae: in early larvae the effect was not clear (the only significant difference was 34 vs 23 psu, Tukey's test $P < 0.001$) (Fig. 2a) but in late larvae development at 12 psu was clearly longer when compared with 23 and 34 psu (Tukey's test, both $P < 0.001$) (Fig. 2a).

Most larvae from the three types at any rearing condition developed through 5 or 6 zoea stages and only 1.6% did it through 4 stages and 2.6% through 7 stages (Table 2). Temperature and salinity interacted with larval type ($P < 0.001$ in both cases). Then GLM was performed separately for each larval type. Most early larvae reached the juvenile phase through 5 stages besides the interaction existent between temperature and salinity (Fig. 2b) (Table 3), and the only significant differences in Tukey's test contrasts were 20 °C/34 psu, and 20 °C/12 psu ($P =$

0.0019) and 20 °C/34 psu, and 20 °C/23 psu ($P = 0.029$). Middle season larvae had a development pattern more variable than early larvae, it was affected only by temperature and with no interactions (Table 2). Whereas half of the larvae reached juvenile phase after 5 stages at 20 °C, 85% did it at 25 °C (Fig. 2b). Finally, the number of stages to reach juvenile phase in late larvae varied with temperature and salinity independently (Table 2). Temperature effect was similar to that on middle season larvae (39% passed through 5 stages at 20 °C, while 84% did it at 25 °C). Regarding to salinity, 72% of larvae passed through more than 5 stages at 12 psu differing from 23 and 34 psu (Tukey's test, both $P \leq 0.01$) (Table 2) (Fig. 2b).

The GLMM performed to compare juvenile size (CL) only showed differences among salinities ($P = 0.037$) (Fig. 2c); larvae developed at 34 psu had the longest carapace (CL = 0.965 ± 0.065 mm), at 23 psu CL = 0.939 ± 0.062 mm and at 12 psu CL = 0.936 ± 0.065 mm. Nevertheless, the a posteriori test was unable to separate groups and no interactions were detected among factors. Finally, weight of larvae was also affected by salinity ($P = 0.002$) (Fig. 2d), being the lightest those developed at 12 psu (0.133 ± 0.026 mg). Again, a posteriori comparisons could not separate groups. Furthermore, interaction existed between temperature and larval type ($P < 0.0001$) and the separate analysis of temperature effect showed that early and middle season larvae were heavier at 25 °C ($P < 0.025$ in both periods) while no effects were observed in late larvae ($P = 0.05$).

4. Discussion and conclusions

Larvae of *P. macrodactylus* from Mar del Plata harbor were able to complete development, from hatching to metamorphosis, in a salinity range from 12 to 34 psu at both temperatures, 20 and 25 °C. Most adult crustaceans tolerate ranges of temperature and salinity wider than larval stages (Charmantier, 1998; Sastry, 1983). In the oriental shrimp, females were able to survive and develop their ovaries in salinities ≥ 5 psu, but embryonic development was possible in the same salinity range than larvae (12–34 psu) (Vázquez et al., 2013b). In addition, larvae hatched at the beginning, in the midpoint and at the end of the reproductive season have different patterns of use of metabolizable energy, presumably as an adaptation to the conditions prevailing at hatching (Vázquez et al., 2013b).

This study shows that temperature and salinity had different effects on early, middle season and late larvae that may be related to the conditions where females grew and developed its ovary and embryos. Water temperature at Mar del Plata coast starts to rise from its winter minimum in late September, increases until February, the time of highest and less variable temperatures, and begin to fall in March (Servicio Meteorológico Nacional, Argentina). In this way, early and, to a lesser extent, middle season females, their embryo and larvae, experience temperatures lower than late individuals. At the same time, even when Mar del Plata harbor is a typical marine environment with no permanent freshwater input, rains are maximal from November to January and fall to a minimum in February. Although no records are available about daily salinity fluctuations in the area, it seems probable that females and larvae experience more events of low salinities at the beginning and in the midpoint that at the end of the reproductive season. Accordingly, early larvae were the least affected by low temperature (the difference in development time between 20 and 25 °C was minimal compared with middle season and late larvae) and no clear effect of salinity was observed, experiencing only small changes in time and pattern of development at any tested condition. Middle season larvae were affected by low temperature (extending the development and increasing the number of molts), but not by salinity changes; and late larvae presented the more extended development and highest number of larval stages in response to low temperature and low salinity.

Little (1969) collected females of *P. macrodactylus* from brackish water (50 to 70% seawater) but reared larvae successfully in marine water. This author compared larvae from two different periods, summer

Table 1

Results of GLM used to evaluate the effect of temperature and salinity over time to complete larval development from hatching to juvenile phase in larvae from early, middle season and late in the reproductive season.

Type of larvae	Source	χ^2	df	Pr ($>\chi^2$)
Early	Temperature	189.389	1	<0.0001
	Salinity	17.386	2	0.0001
	Temperature \times salinity	5.289	2	0.0710
Middle	Temperature	267.7430	1	<0.0001
	Salinity	3.3118	2	0.19092
	Temperature \times salinity	5.2137	2	0.07377
Late	Temperature	364.9301	1	<0.0001
	Salinity	33.8801	2	<0.0001
	Temperature \times salinity	0.8526	2	0.6529

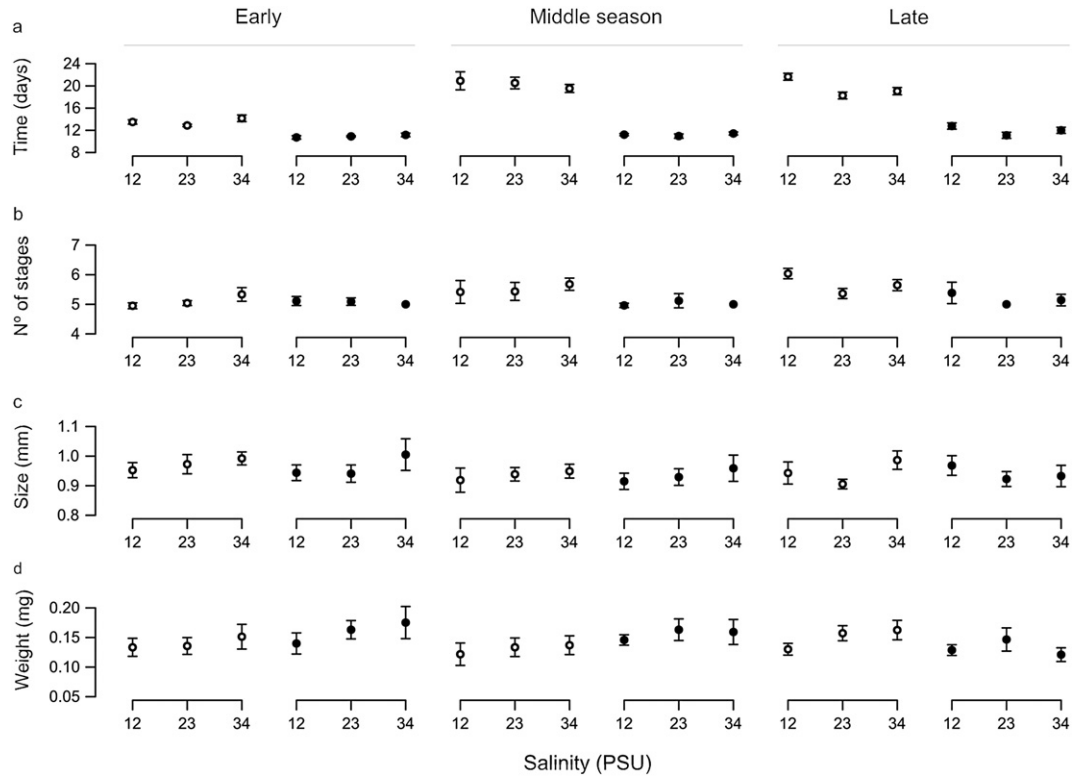


Fig. 2. *Palaemon macrodactylus*. Effect of salinity and temperature on larvae hatched at the beginning, midpoint and end of the reproductive season (early, middle season and late larvae) cultured at three salinities (12, 23 and 34 psu) and two temperatures (20 °C and 25 °C). a. Duration of larval development, b. number of stages to reach the juvenile phase, c. carapace length of juveniles and d. weight of juveniles (mean values \pm 95 confidence interval).

and fall, and reported differences in the time and the number of molts to complete larval development. Even when the experiments of Little (1969) and those reported in this study are not directly comparable, both reflect the high larval variability of this species and suggest that the conditions faced by females during ovarian development and/or by the embryos could be of paramount importance for larval performance. These results the perspective that *P. macrodactylus* is a species with high physiological and developmental plasticity as was previously suggested (Vázquez et al., 2013b) and as has been demonstrated in other palaemonid shrimps (González-Ortegón et al., 2013).

Carapace length of juveniles was not affected by the larval type but depended on the rearing salinity. Also, weight of juveniles depended on salinity and the combined effect of temperature and larval type. As a result, low salinity (12 psu) and, in early and middle season larvae, low temperature (20 °C) produced lighter and smaller individuals, reinforcing the idea that those conditions entail additional metabolic costs. At the same time, those individuals tended to have more larval

stages. It has been documented for different species of palaemonids that stressing factors (as extreme temperatures and salinities or unsuitable food) cause an increase in the number of stages (Anger, 2001; González-Ortegón et al., 2014).

Zoea I did not die immediately at 5 psu suggesting that this stage is able to survive at least some days in low salinities as has been observed in estuarine crabs with a larval export strategy. First zoea of *Neohelice granulata*, for example, unlike the following stages, can survive several days at low salinities (around 5 psu) and the ability to tolerate low salinities is acquired again by the megalopa; this developmental strategy provides newly hatched larvae the time necessary to migrate to coastal marine waters with higher salinities (Anger et al., 1994, 2008; Bas et al., 2007). A decreased range of salinity tolerance as larval development progress has also been documented in three palaemonid species: *Palaemon serratus*, *P. longirostris* and *Palaemonetes varians* (Antonopoulou and Emson, 1989). According to their results, *P. varians* would be the only species of the three capable of reaching the juvenile phase in estuarine conditions, while the other two require marine conditions before metamorphosis.

Table 2

Number of stages from hatching to juvenile phase in early, middle season and late larvae, cultured at different combinations of temperature and salinity.

Larval type	No. of stages	20 °C			25 °C		
		12	23	34	12	23	34
Early	4	1	0	0	0	0	0
	5	19	23	17	16	22	6
	6	0	1	6	2	2	0
Middle season	7	0	0	1	0	0	0
	4	0	1	0	1	3	0
	5	8	13	10	26	16	14
Late	6	3	7	17	0	6	0
	7	1	2	1	0	0	0
	4	0	0	0	0	0	0
	5	2	21	13	9	10	12
	6	21	12	20	3	0	2
	7	3	0	1	1	0	0

Table 3

Results of GLM used to evaluate the effect of temperature and salinity over the number of stages from hatching to juvenile phase in larvae from early, middle season and late in the reproductive season.

Type of larvae	Source	χ^2	df	Pr ($>\chi^2$)
Early	Temperature	0.0977	1	0.7545
	Salinity	9.8379	2	0.0073
	Temperature \times salinity	7.1093	2	0.0285
Middle	Temperature	13.2823	1	0.0002
	Salinity	3.0110	2	0.2219
	Temperature \times salinity	1.1243	2	0.5699
Late	Temperature	28.0400	1	<0.0001
	Salinity	35.3484	2	<0.0001
	Temperature \times salinity	0.4891	2	0.783

P. macrodactylus has been recorded mainly in brackish water (Béguer et al., 2011; González-Ortegón et al., 2006; Little, 1969). A spatial segregation of developmental stages seems to exist in the Gironde estuary (France); zoea I, and especially zoeae II to IV, were scarce in the outer estuary (5 to 23 psu salinity), while zoea V was well represented; post-larval stages (sic) and juveniles were abundant in the inner estuary, with salinities between 0 and 6 psu (Béguer et al., 2011). Such distribution within the estuary suggests different tolerances among larval stages and a development of the intermediate zoeae in higher salinities. Recently, Torres et al. (2012) reported the presence of *P. macrodactylus* larvae in marine waters of the western Mediterranean, suggesting that the life cycle strategies of this species could include exporting zoeae to offshore marine areas, increasing their dispersal capacity in relation to estuarine species that spend their entire life cycle in brackish waters. In accordance with the evidence from European populations, the reproductive studies performed with the marine population at Mar del Plata harbor showed an optimum for ovarian and embryo development at an intermediate salinity (12 psu) (Vázquez et al., 2013a), even when females were able to survive at lower salinities (5 psu). In contrast, larval development showed the same performance between marine and intermediate salinities and survival did not occur at 5 psu, suggesting different selection pressures between adults/embryos and larval stages, probably associated to broader movements of larvae related to a strategy of “exportation” to high salinity conditions.

In conclusion, the results obtained here demonstrate that *P. macrodactylus* larvae tolerated a narrow range of salinity when compared with adults. However, taking into account the marine conditions of Mar del Plata harbor and the plasticity of responses observed, we cannot exclude the possibility that larval performance may be enhanced through acclimation of females and/or embryos to low salinities, extending somewhat the range of tolerance of the different stages of development. Furthermore, the tolerance range, and the effect of acclimation on each larval stage needs to be determined before formulate predictions about the distribution of larvae in different environments and the ability of the species to successfully complete their life cycle in estuarine habitats.

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