

Seasonal variation in reproductive traits of the oriental shrimp *Palaemon macrodactylus* (Crustacea: Caridea: Palaemonidae) in a non-native population

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Abstract The magnitude of variations in reproductive traits of *Palaemon macrodactylus* females throughout a breeding season was studied in a non-native population at Mar del Plata harbor, Argentina. Fecundity, egg size, reproductive output, weight and elemental composition of eggs, and larvae were analyzed in females collected at the beginning, in the mid point, and near the end of a reproductive season and designated as early, middle season, and late females. The highest reproductive output was observed in early females, while the highest fecundity and egg volume occurred in middle season females. Eggs and larvae showed larger body mass in early than in late females. Embryos from early females contained and consumed more carbon during development than embryos from late females, and they also used part of the available nitrogen. Differences in reproduction were observed among the three groups of females. On the one hand, late females matured early but had a poor first reproduction, with few embryos and high egg loss; however, they had longer reproductive life and an enhanced reproductive output in the following season when they became early females. On the other hand, females collected at the midpoint in the reproductive season matured later and had the highest fecundity and egg volume. In addition, larvae with different characteristics resulted from each type of female and were presumably well adapted to the conditions prevailing at the moment

they hatched. The extended reproductive period and the diversity of embryos and larvae produced may favor the invading ability of the species.

Keywords *Palaemon macrodactylus* · Invasive species · Intraspecific variation · Elemental composition

Introduction

The potential for the introduction of a species into new habitats or areas is given by their propagule pressure, i.e.: the number of individuals of that species released into the new area (Carlton 1996; Simberloff 2009; Lockwood et al. 2005). The ability of propagules to survive transport, usually early life stages in marine species, is vital for an eventual establishment of the species (Johnston et al. 2009). Females that may have experienced different environmental conditions in an extensive reproductive season produce larvae at different times throughout the season (Gomi et al. 2008). Consequently, such species produce propagules with varying characteristics, increasing the possibilities of success of some of them in the new area at a given set of conditions (Johnston et al. 2009). Furthermore, a long reproductive season should confer an advantage with respect to local species with shorter spawning periods (MacInnis and Corkum 2000).

After successive introductions, presumably due to marine traffic, the oriental shrimp *Palaemon macrodactylus* (Rathbun 1902), native of coastal areas in Japan, Korea, and northern China (Newman 1963), has successfully invaded Pacific and Atlantic coasts of the United States, Europe, and Australia (Newman 1963; Jensen 1995; Ashelby et al. 2004; Cuesta et al. 2004; d' Udekem d' Acoz et al. 2005; González-Ortegón and Cuesta 2006; Béguer

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et al. 2007; Chicharo et al. 2009; Micu and Niță 2009; Raykov et al. 2010; Lavesque et al. 2010; Warkentine and Rachlin 2010; Soors et al. 2010). Although it is commonly associated with brackish water estuarine areas (Béguer et al. 2011), the first record of the species in the south-western Atlantic was from Mar del Plata harbor, Buenos Aires Province, Argentina (Spivak et al. 2006), where fully marine conditions prevail. Recently, Martorelli et al. (2012) discovered three new invaded sites in Argentinean coasts: Bahía Samborombón, Bahía Blanca, and the mouth of Río Negro, all of them estuarine environments.

The colonization of brackish water by *P. macrodactylus* may be facilitated by the strong osmoregulatory capacity showed by adults (Born 1968; González-Ortegón and Cuesta 2006), but this capacity alone is not enough to explain the success of newly settled populations. The actual characteristics associated with the timing of reproductive maturity and fecundity enhance the success of invasive species (Johnston et al. 2009). Omori and Chida (1988a, b) studied the life history and reproduction of *P. macrodactylus* in a native population from Japan. Differences in egg volume, fecundity, and reproductive output of females belonging to different cohorts were reported, and it was suggested that they could represent different adaptive strategies in the preservation of the species.

The life history of the recently established population in Mar del Plata harbor has just been studied (Vázquez et al. 2012). Some traits (life span, maximal size, and size at maturity) differed from the native estuarine population in Japan, and also, a decrease in the size of reproductive females during the breeding period was observed. At the beginning of the breeding season (October–November), reproductive females were represented only by the largest individuals. Later (December–January), an intermediate size group appeared as reproductive specimens. The largest females sustained this condition, but the group of middle-sized females reached maturity and began their reproductive stage. Finally, large females died and a new group of small females developed into the reproductive population (February–March), being the only reproductive group at the end of the season (Vázquez et al. 2012).

The aim of this study was to determine whether size differences observed throughout a breeding season in reproductive females of *P. macrodactylus* from the Mar del Plata population could be associated with changes in reproductive traits (fecundity, egg size, reproductive output, weight, and chemical composition of eggs and larvae). Such variations may represent distinct strategies of successive groups of females to maximize their reproductive performance, and they may also be one of the reasons for the success in invading new areas.

Materials and methods

The study was carried out in Mar del Plata harbor (38°03'S; 57°31'W) Buenos Aires, Argentina, where monthly average salinity ranges from 32 to 33.7 psu (Schwindt et al. 2010) and monthly average temperature ranges from 9.3 °C in July to 20.9 °C in February (Servicio de Hidrografía Naval). Shrimps were collected with a hand net, 300- μ m mesh, inside an area used for sailing activities.

The sampling schedule was based on a previous study of the same population which demonstrated that reproductive females were large at the beginning, intermediate in the middle, and small at the end of the reproductive season (Vázquez et al. 2012). Consequently, ovigerous females were sampled in those three different moments along the reproductive season and called: early, middle season, and late females depending on the time of collection. Early females were collected in October–November, middle season females in December–January, and late females in February–March (see detailed collection dates below). Eggs and larvae obtained from each type of females were named as early, middle season, and late eggs or larvae, respectively.

Fecundity

Absolute (number of eggs) and relative (number of eggs/size) fecundity were estimated from at least 40 females collected on the following dates: October 30 and November 26, 2007 (early females), December 28, 2007 and January 25, 2008 (middle season females), and February 27 and March 28, 2008 (late females). All females were sized (carapace length, CL), and the egg mass of each was extracted. Eggs were counted and embryos assigned to one of the two categories: stage I, yolk occupying 70–100 % egg volume, embryos undifferentiated; stage II, yolk occupying less than 70 % egg volume, eyes visible. Since eggs were easily damaged when freshly manipulated, ovigerous females were first preserved in formalin 4 % for three days before extracting the egg mass. Fecundity was estimated separately for females with stage I and stage II embryos, to evaluate egg loss.

Reproductive output and egg volume

Reproductive output, defined as dry weight of egg mass/dry weight of female (Clarke et al. 1991), was estimated from 30 females with stage I eggs collected on October 28, 2008 (early females), on December 27, 2008 (middle season females) and on February 22, 2009 (late females). Females were fixed as previously indicated, and each female and their egg mass were then separately dried (48 h, 60 °C) and weighted. Egg volume was estimated from 10 eggs freshly extracted from 5 early, 5 middle, and 5 late females, as the volume of an ellipsoid

($V = d^2 \times D \times \pi/6$), where d and D are the minor and major diameter, respectively (Corey and Reid 1991). Eggs were kept in a drop of marine water on a slide to avoid shrinking; d and D were measured using a SZ40 Olympus stereo microscope furnished with a micrometric eyepiece with an accuracy of 0.01 mm. The average volume was calculated for each female.

Weight and elemental composition of eggs and larvae

These variables were determined in 5 females with ripe ovaries and 5 females with advanced embryos captured on October 23, 2009 (early females), January 12, 2010 (middle season females), and March 2, 2010 (late females). Females with ripe ovaries were kept in the laboratory until extrusion of egg mass. Then, 3 replicates of 20 eggs per female were put into previously weighted 8 × 5 mm tin capsules and lyophilized. Dry weight (DW), content of carbon (C), and nitrogen (N) were measured in a CN elemental analyzer (Thermo Finnigan Flash EA 1112). Females with advanced embryos were kept until larval hatching that occurred 1 or 2 days after collection; the same procedure previously described was used to evaluate DW, carbon, and nitrogen content of 20 freshly hatched larvae per female (3 replicates).

Statistical procedures

Initial and final fecundity (stage I and stage II embryos, respectively) were compared computing linear regression lines of egg number plotted on CL of early, middle, and late ovigerous females and using an analysis of parallelism and ANCOVA. Since the size range of late females do not overlap with early and middle season females, relative fecundity—instead of absolute fecundity—was compared with one-way ANOVA. Data were pooled when no differences appeared between final and initial fecundity. Otherwise, only females with stage I embryos were used for comparison. Reproductive output was compared among early, middle season, and late ovigerous females with a one-way ANOVA, while egg volume, dry weight, N and C content, and the C:N relation of eggs and larvae were compared with a two-level nested ANOVA with type of female as fixed factor and female as nested factor. When the assumptions were not met, one-way ANOVAs were performed. When ANOVA indicated significant differences between groups, a Tukey’s test was subsequently performed (Zar 2010).

Results

A linear relationship existed between number of eggs and carapace length of females with stage I or stage II embryos

from early, middle, and late females of the reproductive season (Table 1). Egg loss was not apparent in early and middle season females, since no differences were observed in fecundity parameters between those with stage I and stage II embryos (ANCOVA $F = 2.24$, $P = 0.13$ for early females and $F = 0.0069$, $P = 0.93$ for middle season females; Fig. 1); therefore, data from females with embryos in all stages were pooled. The slope of late females with stage II embryos, instead, was lower than that with stage I embryos (Homogeneity of slopes model, $F = 11.11$, $P = 0.0014$). However, a great egg loss was registered in some, but not in all, late females (Fig. 1) and only those with stage I embryos were considered to compare fecundity with early and middle season females. Absolute average fecundity was 523 eggs (range: 38 to 1,612 eggs). Since the size range of late females did not overlap completely with the size range of the other females, relative fecundity was preferred for a comparison among the three types of females. Maximum relative fecundity was 58.4 % higher than minimum relative fecundity, and the following pattern was observed: middle season > early > late (Fig. 2a; ANOVA, $F = 66.75$, $P < 0.001$; Tukey’s test, all $P \leq 0.001$).

Reproductive output varied among early, middle season, and late females (one-way ANOVA, $F = 4.89$, $P = 0.01$). The maximum reproductive output corresponded to early

Table 1 *Palaemon macrodactylus*: lineal regression parameters of carapace length versus egg number from early, middle season, and late females with eggs in stage I and II of development

Egg stage	Female type	Intercept	Slope	<i>n</i>	<i>r</i> ²	<i>P</i>
I	Early	−495.01	117.56	59	0.271	<0.001
II	Early	−563.37	133.26	21	0.437	<0.001
I	Middle season	−1,422.6	252.65	31	0.548	<0.001
II	Middle season	−1,484.2	259.95	26	0.580	<0.001
I	Late	−856.54	181.13	43	0.758	<0.001
II	Late	−208.71	74.02	26	0.189	0.026

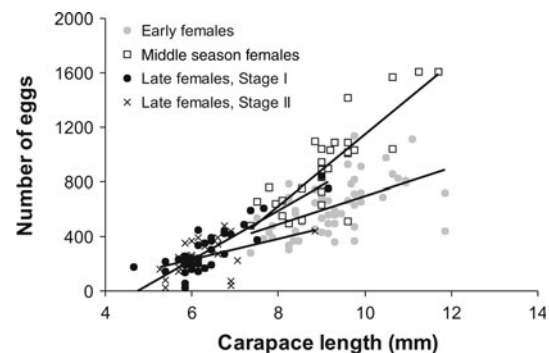


Fig. 1 *Palaemon macrodactylus*: relationship between carapace length and fecundity (number of eggs carried by each female) of early, middle season, and late females. Late females presented different regressions according to egg stage

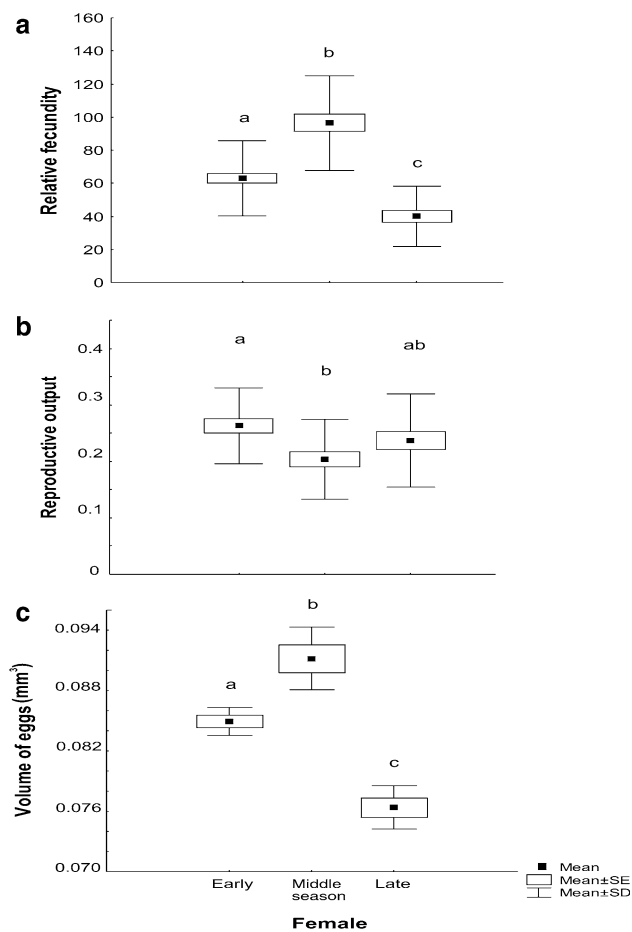


Fig. 2 *Palaemon macrodactylus*: **a** relative fecundity (number of eggs/carapace length), **b** reproductive output (dry weight of egg mass/dry weight of female), and **c** egg volume from early, middle season, and late females. Mean value (black squares), standard error (boxes), and standard deviations (vertical lines) are shown. Different letters represent statistically significant differences

females and differed from the minimum, recorded in middle season females, which was 22.5 % lower (Tukey's test, $P = 0.007$), while no differences were detected between early and late or middle season and late females (Tukey's test, $P = 0.37$ and $P = 0.20$, respectively; Fig. 2b). Egg volume also differed among early, middle season, and late females (Table 2); the largest eggs were on average 19.4 % larger than the smallest ones and egg volume followed the next pattern: middle season > early > late (Fig. 2c; Tukey's test, all $P < 0.01$).

The analysis of egg samples from middle season females failed, and in consequence, only eggs from early and late females could be compared. Early eggs were 33.15 % heavier than late eggs (Table 2; Fig. 3a). Carbon content was lower in late than in early eggs (Table 2; Fig. 3b), while N content was similar (Table 2; Fig. 3c). As a result, the C:N ratio was higher in early eggs (Fig. 3d).

Larval weight differed among early, middle season, and late females (Table 2). The maximum difference in the

Table 2 *Palaemon macrodactylus*: Two-level nested ANOVA evaluating differences in volume, dry weight and elemental composition of eggs stage I, and dry weight and elemental composition of larvae stage I among type of female and brood or hatch, nested within type of female

Biomass parameters	Factor	SS	df	MS	F
Egg volume	Female type	0.0055	2	0.0027	51.08**
	Brood (female type)	0.0006	12	0.00005	0.72
	Error	0.0102	135	0.00007	
Egg dry weight	Female type	0.0017	1	0.0017	59.17**
	Brood (female type)	0.0002	8	0.00002	17.15**
	Error	0.00003	20	0.000002	
Egg carbon content	Female type	4,919	1	4,919	5.37*
	Brood (female type)	7,327	8	916	2.50*
	Error	7,336	20	367	
Egg nitrogen content	Female type	25.9	1	25.9	0.58
	Brood (female type)	354	8	44.3	10.31**
	Error	85.8	20	4.3	
Larval dry weight	Female type	0.0008	2	0.0004	7.94*
	Hatch (female type)	0.0006	12	0.00005	40.19**
	Error	0.00004	30	0.00001	
Larval carbon content	Female type	5,386	2	2,693	5.50*
	Hatch (female type)	5,875	12	490	27.0**
	Error	545	30	18	
Larval nitrogen content	Female type	931.2	2	465.6	29.84**
	Hatch (female type)	187.2	12	15.6	10.9**
	Error	43.1	30	1.4	

Significant differences are marked with asterisks (* $P < 0.05$; ** $P < 0.001$)

average weight was 22.6 %, and the following pattern was observed: early > middle season > late (Tukey's test, $P = 0.0001$ in both cases; Fig. 3a). C and N content of larvae also differed along the reproductive season (Table 2; Fig. 3b, c). The maximum average contents were 5.16 and 9.24 % higher than the minimum for C and N, respectively, and the pattern was late > early > middle season for the C content and late > middle season > early for the N content (Tukey's test, all $P < 0.0001$). The C:N ratio also varied among larvae (ANOVA, $F = 23.41$, $P < 0.0001$). As with

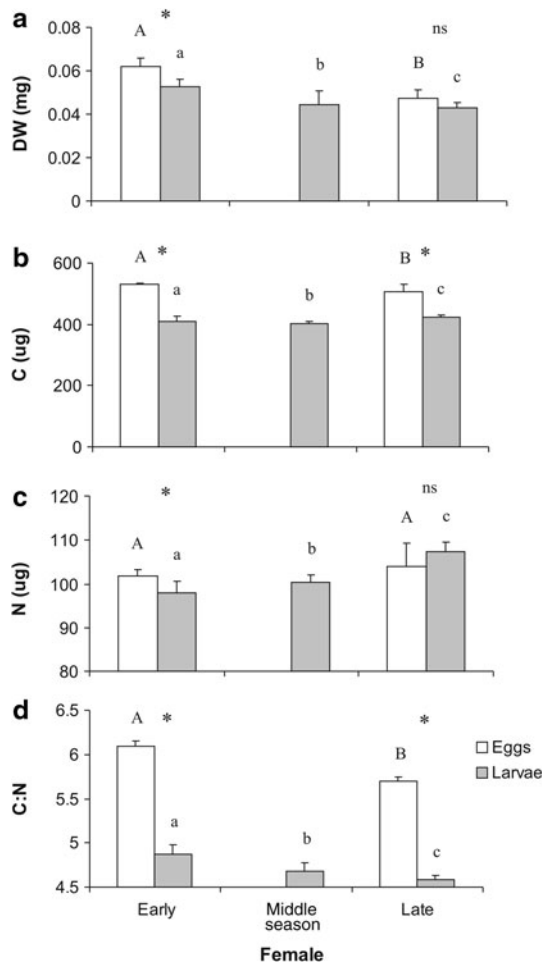


Fig. 3 *Palaemon macrodactylus*: **a** dry weight (DW), **b** carbon content (C), **c** nitrogen content (N), and **d** C:N ratio of eggs stage I and recently hatched larvae (mean ± SD). Eggs and/or larvae corresponded to early, middle season, and late females. *Different capital letters*: statistically significant differences between different type of females; **statistically significant differences between eggs and larvae; ns* nonsignificant differences

eggs, the highest C:N ratio was registered in early larvae, and no differences existed between middle season and late larvae (Tukey’s test, early vs middle season and early vs late, $P < 0.001$; Tukey’s test, middle season vs late, $P = 0.15$; Fig. 3d). Significant differences appeared among broods in all measured variables, excepting eggs volume (Table 2).

When eggs and larvae from early and late females were compared, it was observed that larvae were 15 % lighter than eggs in early females, but they did not differ in late females (T test, $t = 4.082$, $P = 0.004$ and $t = 2.07$, $P = 0.077$, respectively; Fig. 3a). C content decayed throughout the embryonic development, and early and late larvae had 22 and 17 % less C than their respective eggs (Fig. 3b). N content, on the other hand, decayed slightly but significantly (near 4 %) in early larvae but not in late larvae (Fig. 3c). As a result, the C:N ratio of larvae was

much lower than that of embryos (T test, $t = 21.88$, $P < 0.001$; $t = 37.12$, $P < 0.001$ for early and late females, respectively.) (Fig. 3d).

Discussion

The average size of reproductive females of *P. macrodactylus* varied along the annual breeding season in the two sites where data on population structure had been published: Matsushima Bay, Japan and Mar del Plata harbor, Argentina (Omori and Chida 1988a, b; Vázquez et al. 2012).

In the native Japanese population, Omori and Chida (1988a, b) identified three groups of females corresponding to different cohorts that settled in three different years. In the invasive Argentine population, three groups of females were also detected, but they corresponded to shrimps settled at different times in the same breeding season varying in their patterns of growth and maturity (Vázquez et al. 2012). The first settlers of the season grew fast in the warmer months, reached sexual maturity earlier, and reproduced at the end of the same season. They were the small late females, which resume their reproductive activity in the following season as large early females. On the contrary, the last settlers of a season matured at the end of spring during the following season, appearing now as middle females; this process was observed to occur some weeks after early females had started to reproduce (Vázquez et al. 2012).

In this study, we could demonstrate that late females from Mar del Plata had the lowest relative and absolute fecundity and egg volume, but they produced a clutch at the end of the season. Even though this was a less successful brood, with higher egg loss and low number of small larvae, it may represent the possibility of an extra group of settlers. In Japan, where the species probably evolved, the reproductive season is longer, with milder winters, and late settlers produced by the smallest females (Omori and Chida 1988a, b) could represent an advantage for the maintenance of the population. However, it is doubtful that larvae produced by late females in Mar del Plata have always been able to settle successfully, since recruitment finished abruptly at the end of summer concurrently with the disappearance of ovigerous females, at least during the reproductive seasons 2007 and 2008 (Vázquez et al. 2012). In spite of this limitation, late females had a prolonged reproductive activity; they would reproduce again during the following season (now as early females) and increase their relative fecundity (and absolute, since they continued growing up) and egg volume.

The new group of reproductive females that appeared in the middle of the reproductive season (middle season

females) presented very different characteristics. They were not able to reach sexual maturity during the first season (since they presumably settled in the middle and/or at the end of the season) and initiated their ovarian development at the beginning of the following season soon after early females started to reproduce. These middle season females grew slowly but reached maturity at a larger size than late females (Vázquez et al. 2012); they produced the highest number of eggs per size unit, which were also the largest eggs of the season. Yet, the reproductive output of middle season females was significantly lower than that of early females and similar to late females. Egg weight of middle season females could not be estimated, but it may be assumed that their weight was similar to that of late females, since larval dry weight did not differ between these females. In general, the production of large eggs reflects an enhanced maternal energy investment at the cost of reduced fecundity (Allen et al. 2008). In this species, by contrast, the increased fecundity of middle season females without a reduction in egg size (and presumably in weight) and without increasing their reproductive output suggests a better body condition. These females continued growing and would probably produce several consecutive broods until they died at the end of summer when all large females disappeared.

The average fecundity estimated for *P. macrodactylus* at Mar del Plata harbor (528 eggs) did not differ from that reported for the population established at Gironde estuary in France (577 eggs; Béguet et al. 2011). This fecundity value corresponded in both cases to female size of approximately 9 mm of CL. In the source area, females reach larger sizes, and consequently, average fecundity is higher. Nevertheless, fecundity estimated for 9 mm CL Japanese females is similar to that observed in the other populations (Omori and Chida 1988a).

Regardless the date of female collection, egg size of *P. macrodactylus* was smaller in Mar del Plata than in Japan. This may be related to the smaller size adults (Vázquez et al. 2012) or to differences in salinity, since there are evidences of an increase in egg volume at low salinities in many decapod species (e.g.: Mashiko 1983; Giménez and Anger 2001; Lardies and Wehrmann 2001; Fuentes et al. 2010). Although salinity at Matsushima Bay was not reported by Omori and Chida (1988a), it was referred as an estuarine area. Then, the smaller size of eggs from the Mar del Plata population could be a consequence of living in an entirely marine environment.

The production of eggs with different characteristics along the reproductive cycle has been documented in other crustacean species (see Díaz 1980; O’Leary Amsler and George 1984; Paschke et al. 2004; Bas et al. 2007, 2008; Urzúa et al. 2012; Bell and Fish 1996), but factors responsible for such developmental plasticity are, in most cases,

matter of speculation. Differences observed in *P. macrodactylus* females might be simply the result of varied resource investment performed by individuals of different age or size. Nevertheless, larvae resulting from the development of eggs produced at different times had different patterns of use of metabolizable energy. Carbon and nitrogen content and consumption in embryos from the beginning and the end of the reproductive season suggest different metabolic pathways (see Anger 2001, pp. 183–191). Early embryos had more C assigned and consumed, and they also used part of the N, while late embryos consumed less C and N. If temperature changes throughout the reproductive season are considered, females, and recently hatched larvae, face lower temperatures at the beginning than at the end of the season (15 °C, November; 21 °C February; data of average monthly surface water temperature at Mar del Plata harbor, Servicio de Hidrografía Naval). The native and present distribution of *P. macrodactylus* corresponds to temperate latitudes with marked seasonal differences. The higher content of lipids (reflected in C content) recorded in early embryos could be an adaptive plastic response of females to a slower development of embryos in the colder water of the beginning of the season, as observed in other decapod species (Paschke et al. 2004; Bas et al. 2007). Accordingly, development of embryos late in the season seemed to be energetically less expensive, since no dry weight loss was observed in larvae hatched, at that moment, a lesser proportion of C was used and all N was conserved.

In summary, females show contrasting reproductive traits along the reproductive season that could be considered as different reproductive strategies, which allow a maximum larval production per year. At the same time, larvae with different characteristics, resulting from each developmental pattern, are presumably well adapted to the conditions prevailing at hatching. In this way, *P. macrodactylus*, whose adults are able to cope with a broad range of physical conditions, produce a range of embryos and larvae with different characteristics in an extended reproductive season. This gives the species a great chance of spreading propagules when they are transported into different new areas.

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