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Effects of temperature experienced during embryonic development on biomass and C and N composition at hatching in *Palaemon serratus* (Pennant, 1777)

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Abstract

In decapod crustaceans, the conditions experienced during embryonic development trigger phenotypic plasticity of the larvae at hatching. The objective of this study was to test the effects of temperature during embryonic development of *Palaemon serratus* on the phenotypic plasticity of hatching larvae. We incubated egg-bearing females from eggs laying to hatching at four temperatures (10, 15, 18 and 20°C). Weight, carbon and nitrogen contents were measured on newly laid eggs and on freshly hatched larvae. The duration of embryonic development was negatively correlated with incubation temperature. At 20°C, all females abandoned their eggs during development. Incubation temperature had no effect on the weight and the percentage of N of the larvae at hatching, while it did affect their percentage of C and their C/N ratio. Embryos incubated at 10°C seemed to produce larvae with fewer lipid reserves than those incubated at 15 and 18°C. They probably overconsumed their lipid reserves to compensate for the metabolic losses due to the low temperature. These results provide information on the link between maternal investment per egg and larval development in *P. serratus*.

KEYWORDS

C/N, decapod, eggs, larvae, phenotypic plasticity

1 | INTRODUCTION

In decapod crustaceans, the conditions encountered during embryonic development initiate the phenotypic plasticity of the larvae at hatching. The salinity experienced during embryonic development affects the loss of biomass during this phase and the amount of lipids accumulated during the first hours of larval development (Giménez & Anger, 2001; Giménez & Torres, 2002; Laughlin & French, 1989). There is also a

temperature-related pattern of negative correlation between temperature and duration of embryonic development (Wear, 1974). By comparing the size of the stage zoea I of decapods collected between latitudinally distant regions, several authors have hypothesised that the temperature experienced during embryonic development also has an effect on the larval biomass at hatching (Críaes, 1985; Paschke, 1998; Shirley et al., 1987; Thatje & Bacardit, 2000; Wehrmann & Kattner, 1998; Weiss et al., 2010). The negative correlation between embryonic

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incubation temperature and larval biomass at hatching has been verified in the laboratory (Brillon et al., 2005; Smith et al., 2002; Wehrmann & López, 2003). This is partly due to the increase in cardiac and metabolic activity with increasing temperature (García-Guerrero et al., 2003; Naylor et al., 1999; Tills et al., 2022). Embryos “overconsume” their lipid reserves, which are the main source of energy during embryonic development in decapods (Anger et al., 2002; Pandian, 1994; mainly fatty acids in *Palaemon serratus*, Morais et al., 2002). In decapod embryos, carbon (C) and nitrogen (N) content (which have been shown to be good proxies for lipid and protein content; Anger, 1996) and the relative composition of these elements (C/N ratio) are used to study energy metabolism during development (Anger & Harms, 1990; Fischer, Thatje, Graeve, et al., 2009; Giménez & Anger, 2001).

The common prawn, *P. serratus* (Pennant, 1777), is distributed along the European coast (Udekem, 1999). This species is traditionally fished in northwestern Europe (Fahy & Gleeson, 1996; Kelly et al., 2008). As with other *Palaemon* spp., *P. serratus* is an essential component of the trophic structures of the ecosystems in which it lives (Attrill & Thomas, 1996; Sá et al., 2006; Sturbois et al., 2022). This shrimp has a life expectancy of 2–5 years, and the females reproduce twice a year (winter laying then summer laying, Campillo, 1979). Its economic and ecological importance has motivated numerous studies on its larval development, which appears to be plastic in relation to temperature (Baudet et al., 2022; Campillo, 1979; González-Ortegón & Giménez, 2014; Kelly et al., 2012; Lassus & Maggi, 1980; Reeve, 1969b; Yagi & Ceccaldi, 1985). The effect of temperature on the duration of embryonic development has also been studied by several authors in this species whose females carry their eggs for incubation (Campillo, 1979; Forster, 1951; Phillips, 1971; Reeve, 1969a; Richard, 1974; Wear, 1974). Among these authors, only González-Ortegón and Giménez (2014) examined the effects of embryonic incubation temperature on biomass at hatching in *P. serratus* larvae. At their incubation temperatures (12 and 18°C), they showed no effect on this biological trait. The females they used were also already carrying their eggs. To date, only González-Ortegón et al. (2018) have studied the C/N ratio of *P. serratus* eggs but not explored the effects of incubation temperature on bioenergetics.

The objective of this study is to test the effects of temperature experienced during embryonic development on the phenotypic plasticity of *P. serratus* hatching larvae. Understanding these effects will provide information on the relationship between maternal investment per egg and larval development. To this end, we incubated individuals at four different temperatures in the laboratory from adult copulation to larval hatching. We measured biomass and

carbon and nitrogen composition at the beginning and end of embryonic development. We hypothesised that biomass and lipid reserve consumption at hatching decrease with incubation temperature.

2 | MATERIALS AND METHODS

2.1 | Shrimp collection and maintenance

Between 19 January 2021 and 4 March 2021, 40 couples of *P. serratus* were sampled using professional fishing traps at a depth of between 15 and 20 m. The eggs laid at this time of year correspond to the winter laying (Campillo, 1979). Males were selected randomly. Only females with similar body size, mature ovaries (stage 5) and at the end of the moulting cycle (D1^{'''}–D2) were selected for the study (Richard, 1974). On average (\pm SE), their cephalothorax length (from the tip of the rostrum to the posterior dorsal edge of the cephalothorax) was 40.5 (\pm 0.84), 38.5 (\pm 0.64), 39.7 (\pm 0.75) and 40.8 (\pm 1.11) mm at 10, 15, 18 and 20°C, respectively. At the initiation of the experiment, female lengths were similar in the four water baths (Kruskal–Wallis rank sum test, $\chi^2 = 4.4$, $df = 3$, $p = .22$; $N = 10$ per temperature), correspond to females in their second year of life (Campillo, 1979), limiting effect of female size on egg production and size (Emmerson et al., 2017). The shrimp were transferred to the laboratory of the University of Le Havre (Seine-Maritime, France) and slowly acclimatised to the temperature of their water bath (temperature increase in maximum 0.2°C per minute by adding seawater at room temperature, Richard, 1978). Four water baths were filled with 200 L of natural filtered and aerated seawater at a salinity of 30 ppt and regulated at 10, 15, 18 and 20°C, respectively (temperature \pm 0.3°C, regulated by a TECO TK700 cooling unit). Forty pairs of shrimp (male/female) were randomly selected and isolated in wire baskets covered with fine mesh. Ten baskets were then placed in each of the four water baths (Figure 1). The shrimp were then maintained under a 12:12 (L:D) photoperiod and fed individually twice a week ad libitum with squid pieces. The seawater was changed by half three times a week to avoid ammonium increase. Couples were monitored daily, and males were removed after the eggs were laid by the female. Copulation is visible due to the nuptial moult of the female. The female then lays her eggs within 24–48 h (Panouse, 1946). For each water bath, dissolved oxygen (oximeter, Oxyguard), salinity (refractometer), pH (pH-meter, Oxyguard) and ammonium concentration (Visicolor NH4+ and PF12+ spectrophotometer, Hanna Instruments) were measured three times a week.

FIGURE 1 Experimental design to study the effects of temperature on the embryonic development of *Palaemon serratus*. Of the 10 females that laid eggs per condition (i.e. in each of the four water baths), six females incubated their eggs from laying to hatching while the egg masses of the other four females were removed after laying for analysis. The illustrations of the shrimp are modified from the one available on the Muséum-Aquarium de Nancy website by Marion Arbona.

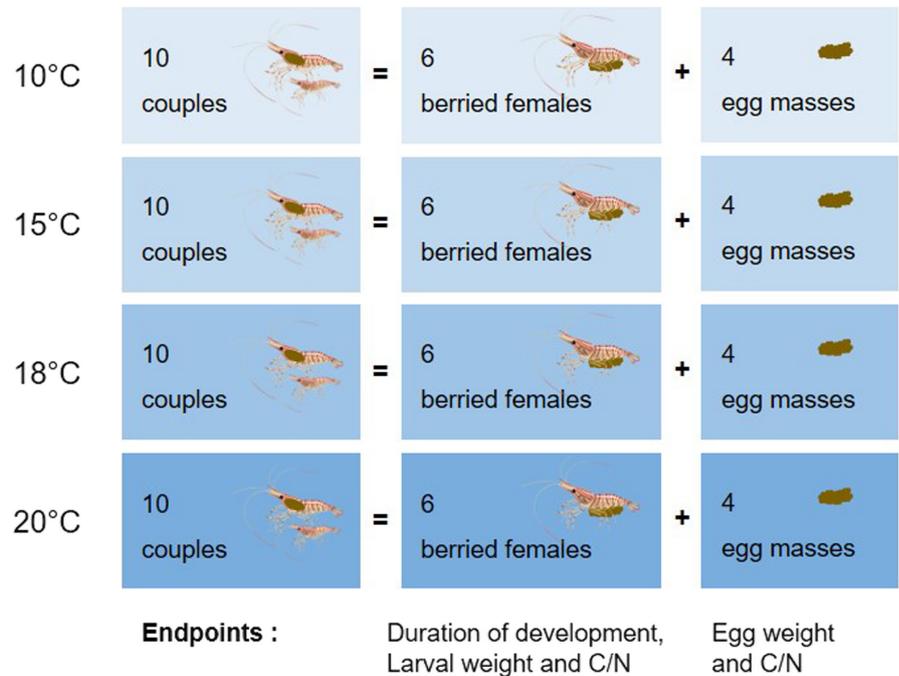


TABLE 1 Average physico-chemical conditions (\pm SD) in the four water baths during maintenance of *Palaemon serratus* couples and incubation of eggs by females.

	10°C	15°C	18°C	20°C
Dissolved oxygen (%)	112.35 \pm 5.75	109.24 \pm 5.74	108.99 \pm 5.03	100.21 \pm 2.78
Salinity (g L ⁻¹)	31.49 \pm 2.08	31.61 \pm 2.15	31 \pm 2.73	32.09 \pm 2.12
pH	8.00 \pm 0.04	8.06 \pm 0.05	8.05 \pm 0.07	8.06 \pm 0.03
Ammonium (mg L ⁻¹)	0.87 \pm 0.59	0.74 \pm 0.54	0.84 \pm 0.71	1.15 \pm 0.67

2.2 | Laying and hatching endpoints

Of the 10 females that laid eggs in each of the four water baths, six females incubated their eggs from laying to hatching while the egg masses of the other four females were removed after laying (Figure 1). For each female from which we removed the eggs on the day of laying, three batches of 100 eggs were weighed and one batch of 20 eggs was rinsed with distilled water and frozen at -80°C . The incubating females were kept under the same conditions as described in the previous paragraph (see Section 2.1). No eggs were removed from them to avoid egg-laying abandonment due to handling stress (Fisher & Clark, 1983). When the eggs from each female hatched, three batches of 100 larvae were weighed and one batch of 10 larvae was rinsed and frozen at -80°C .

2.3 | C and N content

The frozen samples were freeze-dried, ground and weighed to the nearest 0.001 mg using a microbalance (Perkin Elmer AD6 Autobalance). The C and N content was quantified using a CHN elementary analyser (Carlo

Erba NA2100, Thermo Quest CE International). Results were expressed as the mass percentage of the element.

2.4 | Statistical analysis

Statistical procedures were implemented with R software (R Core Team, 2020). To test the effects of temperature on the duration of embryonic development and weight, C, N concentration and C/N ratio of eggs, we used non-parametric Kruskal–Wallis rank sum tests due to the non-normality of the data. Pairwise Wilcoxon rank sum tests with Holm correction were used as post hoc analysis.

3 | RESULTS

3.1 | Embryonic development

The physico-chemical parameters remained stable during the maintenance of the pairs and the incubation of the eggs by the females (Table 1). At 20°C , the females that were incubating eggs abandoned them during embryonic development (after 2–21 days of incubation).

They then moulted and died. Their exuviae showed numerous craters typical of the parasite *Ascophrys rodor* (Campillo & Deroux, 1974). At 10, 15 and 18°C, respectively, the eggs carried by the females hatched after 125.9 (± 1.8), 56 (± 0.4) and 36.5 (± 0.5) days, in mean (\pm SE; Figure 2). The duration of embryonic development decreased with temperature (Figure 2; Kruskal–Wallis rank sum test, $\chi^2 = 15.32$, $df = 2$, $p < .05$; $N = 6$ per temperature).

3.2 | Biomass and C and N content at laying and hatching

No larvae were obtained at 20°C; therefore, we do not report weights and C/N ratios of eggs and larvae at this temperature. From laying to hatching, the weight slightly more than doubled while the percentage of N remained approximately unchanged at all temperatures (Table 2; Figure 3a,c). At 10, 15 and 18°C, the percentage of C decreased by 71%, 78% and 78%, respectively, while the C/N ratio decreased by 66%, 74% and 73%, respectively (Table 2; Figure 3b,d). At laying, the temperature experienced by the 12 females (four broods for each of the other three temperatures) had no effect on egg weight, C and N concentration and C/N ratio (Table 3). The egg incubation temperature (six broods per temperature) did not affect the weight and N concentration of the larvae at hatching, but it did affect the C concentration and C/N ratio (Table 3). The C concentration and C/N ratio of larvae hatched at 15 and 18°C are different from those of larvae hatched at 10°C.

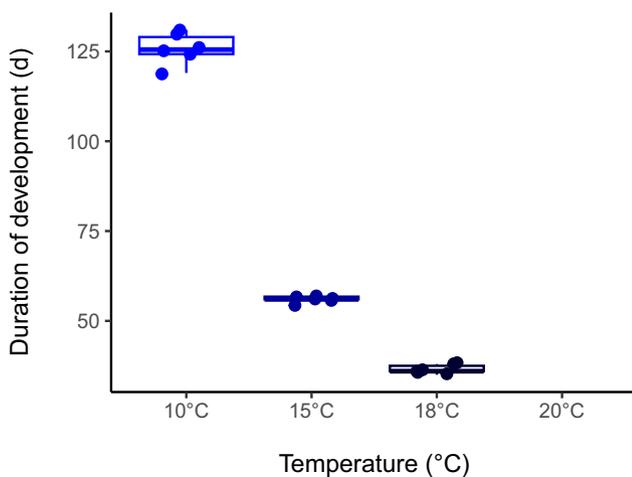


FIGURE 2 Duration of embryonic development (days) of *Palaemon serratus* broods incubated in the laboratory at four constant temperatures (10, 15 and 18°C, $N = 6$ broods per temperature; 20°C, $N = 0$ brood hatchings). The values of each brood are represented with solid circles.

4 | DISCUSSION

The main aim of this study was to investigate the embryonic development of *P. serratus*, especially the effects of incubation temperature on phenotypic plasticity at hatching. At 20°C, egg incubation failed as the females abandoned their eggs. This heat stress has already been described with *Neocaridina heteropoda* (Tropea et al., 2015). *Palaemon macrodactylus* females also abandon their eggs at low salinity (Vázquez et al., 2013). Here, we cannot determine whether egg abandonment at 20°C was caused by heat stress, by the spread of the *A. rodor* parasite throughout the water bath, or by both. Campillo (1979) observed the same parasite with *P. serratus* in the laboratory and found that the shrimp were more parasitised in relatively warm water. It is nevertheless possible to incubate *P. serratus* eggs at 20–21°C (50% hatching in Reeve, 1969a; 96% in Phillips, 1971; 50% in Wear, 1974).

As in other decapods, the duration of embryonic development in *P. serratus* is negatively correlated with incubation temperature (Wear, 1974). At 10, 15 and 18°C, the eggs hatched after approximately 126, 56 and 37 days. These durations are comparable to those reported by other authors, that is 120–140 days at about 10°C, 55–58 days at 15°C and 39 days at 18°C (Forster, 1951; Phillips, 1971; Reeve, 1969a; Richard, 1974; Wear, 1974).

While the embryos increased in biomass during their development, their C and C/N ratio decreased. This suggests that the embryos have consumed the lipid fraction of their biomass during development (Anger, 1996; Brillon et al., 2005; Fischer, Thatje, Graeve, et al., 2009). We had wrongly assumed that the C/N ratio of hatching larvae would decrease with incubation temperature. On the contrary, it was lower at 10°C than at 15 and 18°C, suggesting a higher consumption and an additional energy requirements of lipid reserves at 10°C (Anger & Harms, 1990). Embryos incubated at 10°C drew on their lipid reserves to compensate for the metabolic loss (Holland, 1978). Temperatures of 15 and 18°C should therefore be close to the optimal temperature for embryonic development of *P. serratus* (García-Guerrero, 2010), whereas 10°C should be a suboptimal temperature. Tills et al. (2022) measured the heart rate and estimated the metabolic rate of *P. serratus* eggs at three developmental stages at 15 and 20°C using an energy proxy trait approach. Although heart rate increased with temperature, they estimated that the overall energy expended by an embryo did not vary between these two temperatures. These results partly explain why energy consumption was the same at 15 and 18°C in our experiment. With *P. serratus*, Wear (1974) obtained at least 50% hatching between 12.5 and 21°C and no hatching at 5, 7.5, 10, 25, 27.5 and 30°C. At these lower or higher temperatures, the amount of reserves could have become

TABLE 2 Weight (mg ind⁻¹), proportion of C, N (%) and C/N ratio of eggs at laying and larvae at hatching according to incubation temperature in *Palaemon serratus* (mean, \pm SE); $N = 12$ for eggs and $N = 6$ per temperature for larvae.

	Eggs at laying	Larvae at hatching		
		10°C	15°C	18°C
Weight (mg ind ⁻¹)	0.15 \pm 0.01	0.31 \pm 0.01	0.32 \pm 0.01	0.33 \pm 0.01
Carbon (%)	55.92 \pm 0.06	39.81 \pm 0.3	43.59 \pm 0.16	43.76 \pm 1.2
Nitrogen (%)	10.14 \pm 2.93	10.99 \pm 4.48	10.71 \pm 4.37	10.84 \pm 4.43
C/N	5.52 \pm 0.04	3.63 \pm 0.04	4.07 \pm 0.01	4.04 \pm 0.09

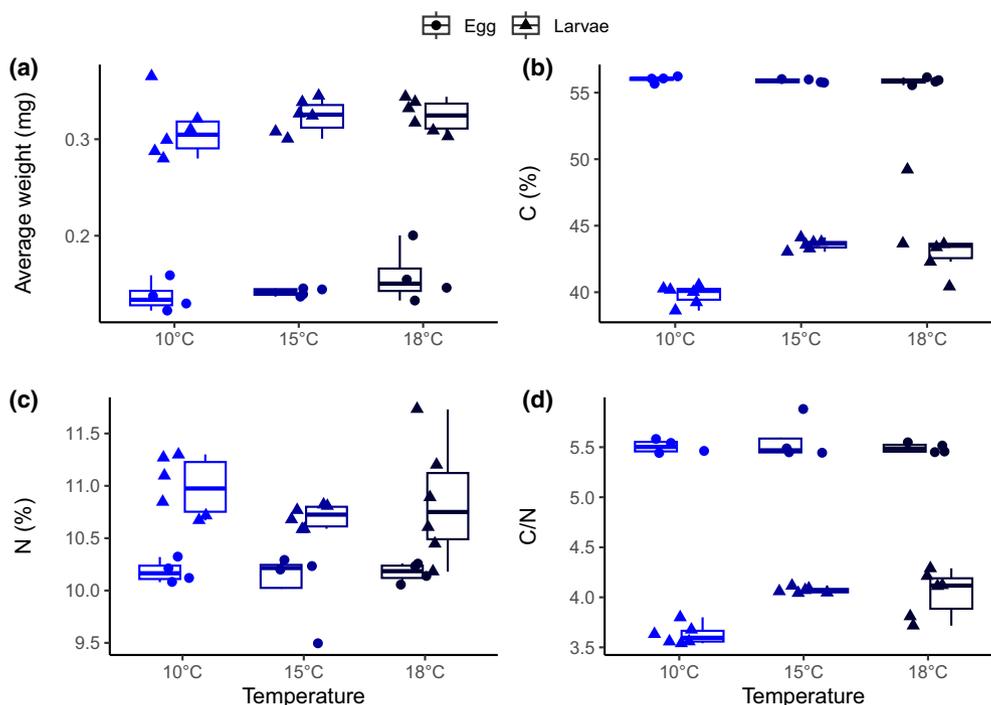


FIGURE 3 Average individual weight (a), proportion of C (b), N (c) and C/N ratio (d) of eggs at laying and larvae at hatching of *Palaemon serratus*. Embryonic development took place in the laboratory at three constant temperatures (10, 15 and 18°C, $N = 4$ groups of 20 eggs and six groups of 10 larvae per temperature). The values of each brood are represented with solid circles (eggs) and solid triangles (larvae).

TABLE 3 Results of Kruskal–Wallis rank sum tests on the influence of incubation temperature on weight, concentration of C, N and C/N ratio of eggs at laying and larvae at hatching of *Palaemon serratus*.

	Eggs			Larvae		
	χ^2	df	p	χ^2	df	p
Weight ~ Temperature	2.20	2	.33	1.98	2	.37
C ~ Temperature	1.43	2	.49	11	2	<10⁻²
N ~ Temperature	0.01	2	1	2.54	2	.28
C/N ~ Temperature	0.12	2	.94	10.98	2	<10⁻³

Bold p's mean that the Kruskal & Wallis Rank Sum test indicates significant effects of incubation temperature on this factor.

limiting and impacted the growth of the embryos (Brillon et al., 2005; Smith et al., 2002; Wehrtmann & López, 2003). In this experiment, the weight of the larvae at hatching

was the same whatever the incubation temperature of the embryos. González-Ortegón and Giménez (2014) also observed no difference in larval biomass at hatching between *P. serratus* eggs incubated at 12 and 18°C. These results lead us to believe that the maximum temperature range chosen in our study was not high enough to cause differences in larval biomass at hatching as observed in other decapod studies (Smith et al., 2002; Wehrtmann & López, 2003). We expected to observe a decrease in larval biomass at hatching after incubation at 20°C.

The larvae have the same weight at hatching, while the duration of development increases with temperature. The growth rate (biomass gain/duration) therefore decreases with temperature (Anger, 1991). The increased consumption of lipid reserves at 10°C (reflected in a decrease in C/N at hatching) is then explained by the increase in total metabolic activity during embryonic development (multiplication of the daily metabolic rate by the number of days

of development). Giménez (2006) discussed the effects of temperature on the rate of biomass loss and on the total biomass loss by changing the duration of embryonic development. Measuring total C and the C/N ratio provides information on the utilisation of lipid resources during embryonic development (Petersen & Anger, 1997). This measurement does not indicate the proportion of lipids that are mainly present and consumed (mostly PUFAs and HUFAs in *P. serratus*, Narciso & Morais, 2001). The type of fatty acid consumed by the embryo may vary in response to temperature (Fischer, Thatje, Graeve, et al., 2009). Temperature can even have an effect on the type of lipids consumed without measuring any difference with the amount of total C (Fischer, Thatje, Graeve, et al., 2009).

We highlighted the decrease in the C/N ratio of hatching larvae when the egg incubation temperature moved away from the optimal temperature. Females of *P. serratus* reproduce twice a year, the winter eggs are incubated between December and May, while the summer eggs are incubated between May and July (Campillo, 1979). Maternal investment per egg varies between the two egg-laying periods of *P. serratus*, with winter eggs having a higher biomass and C/N ratio than summer eggs (González-Ortegón et al., 2018). This seasonal variation in resources per egg is known in temperate decapods, with larger, more lipid-rich eggs at the beginning of the season (Amsler & George, 1984; Bascur et al., 2017; Fischer, Thatje, & Brey, 2009; Urzúa et al., 2012). It is important to note that in winter conditions, the eggs will take several months to develop and the temperature will not be fixed as it is in the laboratory. We measured the decrease in C during the entire embryonic development. Under the environmental conditions, these reserves could mainly be consumed during early development. Furthermore, crustacean embryos may undergo a metabolic shift during ontogeny, with lipids being used preferentially at the beginning of development and proteins at the end (Heilmayer et al., 2008). In the Bay of Seine, *P. serratus* females encounter temperatures of about 6–12°C during incubation of the winter eggs and about 12–20°C for the summer eggs (Claquin et al., 2018). In view of our results, the temperature encountered by winter eggs below the thermal optimum would negatively impact the lipid resources of the larvae at hatching. They would then be expressed on larval performance (Giménez & Torres, 2002; Gomez Diaz, 1987) and even during the juvenile phase (Giménez & Anger, 2003). The larger offspring will be more efficient in the unfavourable conditions of the early season (Petersen et al., 2015), especially more resistant to starvation (Anger & Hayd, 2009). The seasonal difference in maternal investment in *P. serratus* should buffer the temperature-related consumption of reserves (Bascur et al., 2017; Urzúa et al., 2012), allowing females to produce two generations of offspring per season.

5 | CONCLUSION

We have shown that embryonic incubation temperature has effects on developmental duration, bioenergetics and larval phenotype at hatching in *P. serratus*. Further studies are needed to understand the effects of the interaction between incubation temperature and seasonal variation in maternal investment on the plasticity of embryonic development, and the effects reflected in subsequent life stages via phenotypic links (Giménez, 2006; Torres et al., 2020).

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