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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

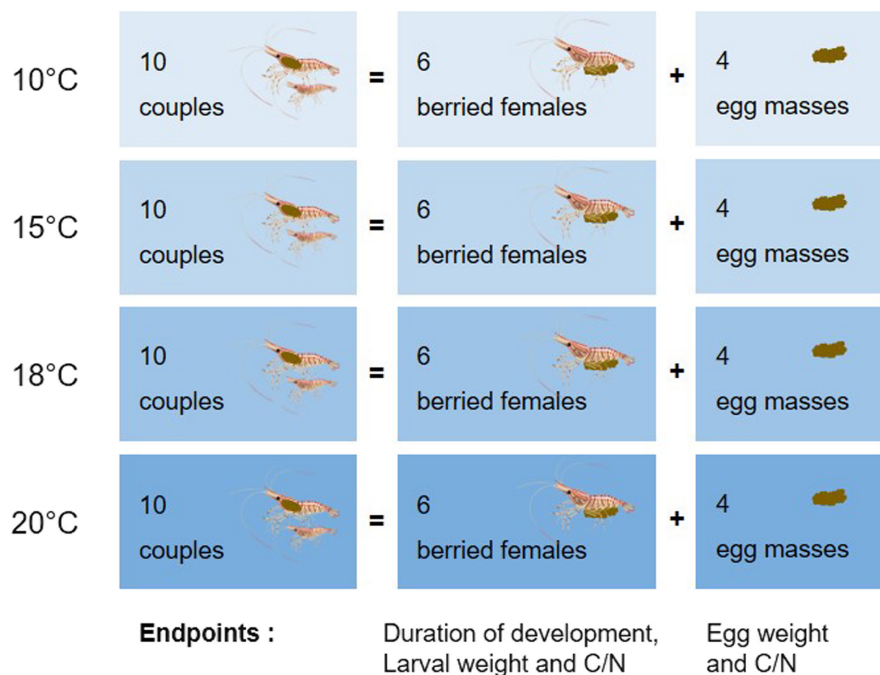
carbon and nitrogen composition at the beginning and end of embryonic development. We hypothesised that biomass and lipid reserve consumption at hatching decrease with incubation temperature.

## 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<sup>'''</sup>–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 <sup>-1</sup> )	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 <sup>-1</sup> )	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  $-80^{\circ}\text{C}$ . 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  $-80^{\circ}\text{C}$ .

## 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  $20^{\circ}\text{C}$ , 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 ( $\pm 1.8$ ), 56 ( $\pm 0.4$ ) and 36.5 ( $\pm 0.5$ ) 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.

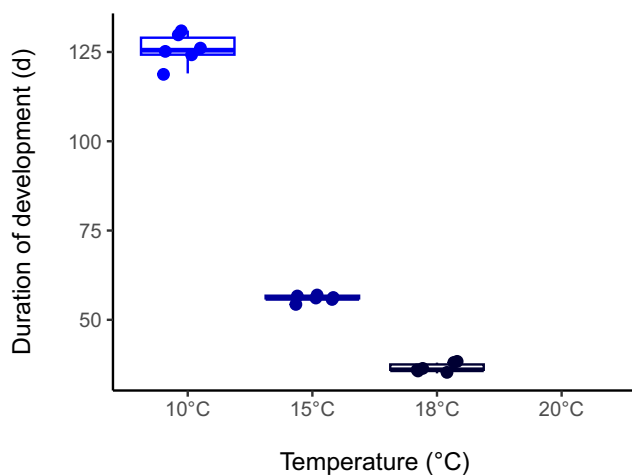


FIGURE 2 Duration of embryonic development (days) of *Palaemon serratus* broods incubated in the laboratory at four constant temperatures (10, 15 and 18°C,  $N = 6$  broods per temperature; 20°C,  $N = 0$  brood hatchings). The values of each brood are represented with solid circles.

## 4 | DISCUSSION

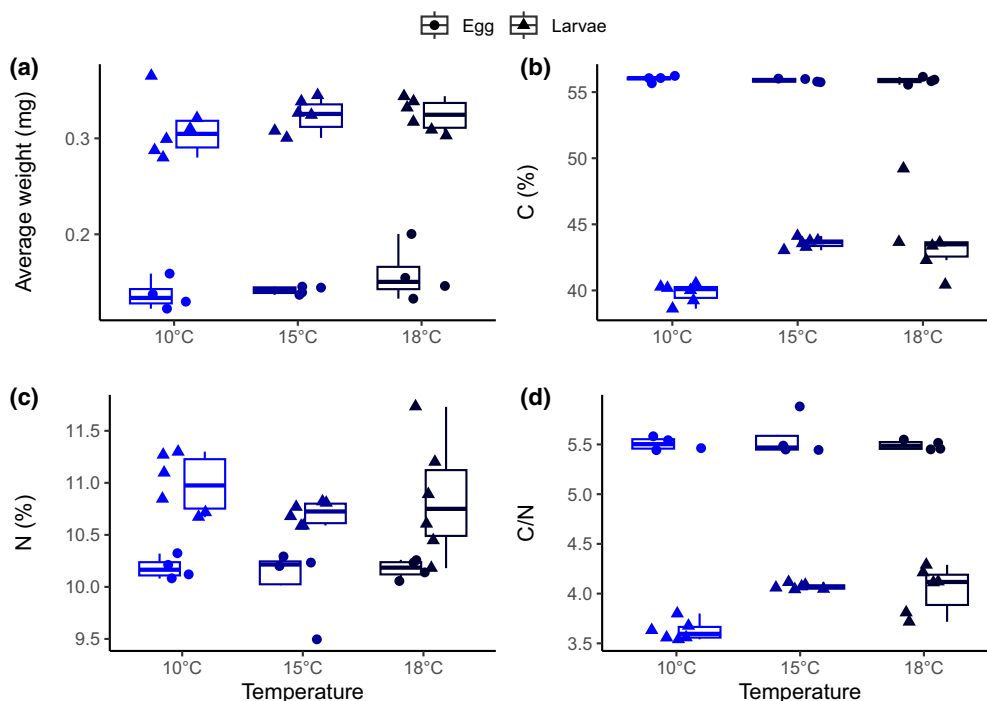
The main aim of this study was to investigate the embryonic development of *P. serratus*, especially the effects of incubation temperature on phenotypic plasticity at hatching. At 20°C, egg incubation failed as the females abandoned their eggs. This heat stress has already been described with *Neocaridina 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<sup>-1</sup>), 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 <sup>-1</sup> )	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		
	$\chi^2$	df	p	$\chi^2$	df	p
Weight ~ Temperature	2.20	2	.33	1.98	2	.37
C ~ Temperature	1.43	2	.49	11	2	<b>&lt;10<sup>-2</sup></b>
N ~ Temperature	0.01	2	1	2.54	2	.28
C/N ~ Temperature	0.12	2	.94	10.98	2	<b>&lt;10<sup>-3</sup></b>

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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## REFERENCES

- Amsler, M. O., & George, R. Y. (1984). Seasonal variation in the biochemical composition of the embryos of *Callinectes sapidus* Rathbun. *Journal of Crustacean Biology*, 4(4), 546–553. <https://doi.org/10.2307/1548068>
- Anger, K. (1991). Developmental changes in the bioenergetics of decapod larvae. *Memoirs of the Queensland Museum*, 31, 289–308.
- Anger, K. (1996). Physiological and biochemical changes during lecithotrophic larval development and early juvenile growth in the northern stone crab, *Lithodes maja* (Decapoda: Anomura). *Marine Biology*, 126(2), 283–296. <https://doi.org/10.1007/BF00347453>
- Anger, K., & Harms, J. (1990). Elemental (CHN) and proximate biochemical composition and decapod crustacean larvae. *Comparative Biochemistry and Physiology Part B: Comparative Biochemistry*, 97(1), 69–80. [https://doi.org/10.1016/0305-0491\(90\)90180-2](https://doi.org/10.1016/0305-0491(90)90180-2)
- Anger, K., & Hayd, L. (2009). From lecithotrophy to planktotrophy: Ontogeny of larval feeding in the Amazon River prawn *Macrobrachium amazonicum*. *Aquatic Biology*, 7(1–2), 19–30. <https://doi.org/10.3354/ab00180>
- Anger, K., Moreira, G. S., & Ismael, D. (2002). Comparative size, biomass, elemental composition (C, N, H), and energy concentration of caridean shrimp eggs. *Invertebrate Reproduction and Development*, 42(2–3), 83–93. <https://doi.org/10.1080/07924259.2002.9652765>
- Attrill, M., & Thomas, R. (1996). Long-term distribution patterns of mobile estuarine invertebrates (Ctenophora, Cnidaria, Crustacea: Decapoda) in relation to hydrological parameters. *Marine Ecology Progress Series*, 143, 25–36. <https://doi.org/10.3354/meps143025>
- Bascur, M., Guzmán, F., Mora, S., & Urzúa, Á. (2017). Seasonal changes in the biochemical composition of females and offspring of red squat lobster, *Pleuroncodes monodon* (Decapoda,

- Munididae), from the Southeastern Pacific. *Marine Ecology*, 38(2), e12419. <https://doi.org/10.1111/maec.12419>
- Baudet, J.-B., Xuereb, B., Dufлот, A., Poret, A., Maniez, E., Le Foll, F., & Coulaud, R. (2022). Temperature-mediated developmental plasticity in winter and summer larvae of *Palaemon serratus*. *Journal of Thermal Biology*, 110, 103343. <https://doi.org/10.1016/j.jtherbio.2022.103343>
- Brillon, S., Lambert, Y., & Dodson, J. (2005). Egg survival, embryonic development, and larval characteristics of northern shrimp (*Pandalus borealis*) females subject to different temperature and feeding conditions. *Marine Biology*, 147(4), 895–911. <https://doi.org/10.1007/s00227-005-1633-6>
- Campillo, A. (1979). *Contribution à l'étude de la crevette rose Palaemon serratus (Pennant): Exploitation, Biologie, Elevage, Epidémiologie* (PhD Thesis). Université des Sciences et Techniques du Languedoc. <https://archimer.ifremer.fr/doc/00000/1196/>
- Campillo, A., & Deroux, G. (1974). *Un nouveau mode de parasitisme externe, aux dépens des arthropodes, chez les ciliés: L'utilisation trophique directe, par Ascophrys rodor, N. G. SP., des strates cuticulaires du test*.
- Claquin, P., Jacqueline, F., Repecaud, M., & Riou, P. (2018). MAREL SMILE buoy data and metadata from coriolis Data Centre (Data set). SEANOE. <https://doi.org/10.17882/53689>
- Criales, M. M. (1985). *Untersuchungen zur Larvalentwicklung von Crangon crangon L. and Crangon allmanni Kinahan (Decapoda, Natantia, Caridea)* (Dissertation).
- Emmerson, J. A., Haig, J. A., Robson, G., Hinz, H., Vay, L. L., & Kaiser, M. J. (2017). Size-selective fishing of *Palaemon serratus* (Decapoda, Palaemonidae) in Wales, UK: Implications of sexual dimorphism and reproductive biology for fisheries management and conservation. *Journal of the Marine Biological Association of the United Kingdom*, 97(6), 1223–1232. <https://doi.org/10.1017/S0025315416000722>
- Fahy, E., & Gleeson, P. (1996). *The commercial exploitation of shrimp Palaemon serratus (Pennant) in Ireland*. <https://oar.marine.ie/handle/10793/794>
- Fischer, S., Thatje, S., & Brey, T. (2009). Early egg traits in *Cancer setosus* (Decapoda, Brachyura): Effects of temperature and female size. *Marine Ecology Progress Series*, 377, 193–202. <https://doi.org/10.3354/meps07845>
- Fischer, S., Thatje, S., Graeve, M., Paschke, K., & Kattner, G. (2009). Bioenergetics of early life-history stages of the brachyuran crab *Cancer setosus* in response to changes in temperature. *Journal of Experimental Marine Biology and Ecology*, 374(2), 160–166. <https://doi.org/10.1016/j.jembe.2009.04.019>
- Fisher, W. S., & Clark, W. H. (1983). Eggs of *Palaemon macrodactylus*: Attachment to the pleopods and formation of the outer investment coat. *The Biological Bulletin*, 164(2), 189–200. <https://doi.org/10.2307/1541138>
- Forster, G. R. (1951). The biology of the common prawn, *Leander serratus* Pennant. *Journal of the Marine Biological Association of the United Kingdom*, 30(2), 333–360. <https://doi.org/10.1017/S0025315400012819>
- García-Guerrero, M., Villarreal, H., & Racotta, I. S. (2003). Effect of temperature on lipids, proteins, and carbohydrates levels during development from egg extrusion to juvenile stage of *Cherax quadricarinatus* (Decapoda: Parastacidae). *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 135(1), 147–154. [https://doi.org/10.1016/S1095-6433\(02\)00354-9](https://doi.org/10.1016/S1095-6433(02)00354-9)
- García-Guerrero, M. U. (2010). Effect of temperature on consumption rate of main yolk components during embryo development of the prawn *Macrobrachium americanum* (Crustacea: Decapoda: Palaemonidae). *Journal of the World Aquaculture Society*, 41(s1), 84–92. <https://doi.org/10.1111/j.1749-7345.2009.00336.x>
- Giménez, L. (2006). Phenotypic links in complex life cycles: Conclusions from studies with decapod crustaceans. *Integrative and Comparative Biology*, 46(5), 615–622. <https://doi.org/10.1093/icb/icl010>
- Giménez, L., & Anger, K. (2001). Relationships among salinity, egg size, embryonic development, and larval biomass in the estuarine crab *Chasmagnathus granulata* Dana, 1851. *Journal of Experimental Marine Biology and Ecology*, 260(2), 241–257. [https://doi.org/10.1016/S0022-0981\(01\)00258-1](https://doi.org/10.1016/S0022-0981(01)00258-1)
- Giménez, L., & Anger, K. (2003). Larval performance in an estuarine crab, *Chasmagnathus granulata*, is a consequence of both larval and embryonic experience. *Marine Ecology Progress Series*, 249, 251–264. <https://doi.org/10.3354/meps249251>
- Giménez, L., & Torres, G. (2002). Larval growth in the estuarine crab *Chasmagnathus granulata*: The importance of salinity experienced during embryonic development, and the initial larval biomass. *Marine Biology*, 141(5), 877–885. <https://doi.org/10.1007/s00227-002-0887-5>
- Gomez Diaz, G. (1987). Effect of environmental embryonic temperature on larval development of *Macrobrachium rosenbergii* (De Man). *Journal of Experimental Marine Biology and Ecology*, 114(1), 39–47. [https://doi.org/10.1016/0022-0981\(87\)90138-9](https://doi.org/10.1016/0022-0981(87)90138-9)
- González-Ortegón, E., & Giménez, L. (2014). Environmentally mediated phenotypic links and performance in larvae of a marine invertebrate. *Marine Ecology Progress Series*, 502, 185–195. <https://doi.org/10.3354/meps10708>
- González-Ortegón, E., Vay, L. L., Walton, M. E. M., & Giménez, L. (2018). Maternal trophic status and offspring phenotype in a marine invertebrate. *Scientific Reports*, 8(1), 9618. <https://doi.org/10.1038/s41598-018-27709-2>
- Heilmayer, O., Thatje, S., McClelland, C., Conlan, K., & Brey, T. (2008). Changes in biomass and elemental composition during early ontogeny of the Antarctic isopod crustacean *Ceratoserolis trilobitoides*. *Polar Biology*, 31(11), 1325–1331. <https://doi.org/10.1007/s00300-008-0470-8>
- Holland, D. (1978). Lipid reserves and energy metabolism in the larvae of benthic marine invertebrates. *Biochem. Biophys. Perspect. Mar. Biol.* 3, 85–123.
- Kelly, E., Tully, O., & Browne, R. (2012). Effects of temperature and salinity on the survival and development of larval and juvenile *Palaemon serratus* (Decapoda: Palaemonidae) from Irish waters. *Journal of the Marine Biological Association of the United Kingdom*, 92(1), 151–161. <https://doi.org/10.1017/S0025315411000415>
- Kelly, E., Tully, O., Lehane, B., & Breathnach, S. (2008). The shrimp (*Palaemon serratus* P.) fishery: Analysis of the resource in 2003–2007. *BIM Fisheries Resource Series*, 8, 48.
- Lassus, P., & Maggi, P. (1980). Etude de la sensibilité thermique des larves du crustacé décapode: *Palaemon serratus* (Pennant). *Revue des Travaux de l'Institut des Pêches Maritimes*, 44, 257–268.
- Laughlin, R. B., & French, W. (1989). Interactions between temperature and salinity during brooding on subsequent zoeal development of the mud crab *Rhithropanopeus harrisi*. *Marine Biology*, 102(3), 377–386. <https://doi.org/10.1007/BF00428490>



- Morais, S., Narciso, L., Calado, R., Nunes, M. L., & Rosa, R. (2002). Lipid dynamics during the embryonic development of *Plesionika martia martia* (Decapoda; Pandalidae), *Palaemon serratus* and *P. elegans* (Decapoda; Palaemonidae): Relation to metabolic consumption. *Marine Ecology Progress Series*, 242, 195–204. <https://doi.org/10.3354/meps242195>
- Narciso, L., & Morais, S. (2001). Fatty acid profile of *Palaemon serratus* (Palaemonidae) eggs and larvae during embryonic and larval development using different live diets. *Journal of Crustacean Biology*, 21(3), 566–574. <https://doi.org/10.1163/20021975-99990158>
- Naylor, J. K., Taylor, E. W., & Bennett, D. B. (1999). Oxygen uptake of developing eggs of *Cancer pagurus* (Crustacea: Decapoda: Cancridae) and consequent behaviour of the ovigerous females. *Journal of the Marine Biological Association of the United Kingdom*, 79(2), 305–315. <https://doi.org/10.1017/S0025315498000332>
- Pandian, T. J. (1994). Arthropoda-crustace. In K. G. Adiyodi & R. G. Adiyodi (Eds.), *Reproductive biology of invertebrates* (pp. 39–166). IBH.
- Panouse, J. B. (1946). *Recherches sur les phénomènes humoraux chez les crustacés: L'adaptation chromatique et la croissance ovarienne chez la crevette Leander serratus*. Faculté des Sciences de Paris.
- Paschke, K. (1998). *Untersuchungen zum Energiestoffwechsel der Nordsee-Garnele Crangon crangon (Linnaeus 1758) (Decapoda: Caridea)* (Dissertation). <https://ci.nii.ac.jp/naid/10022017066/>
- Pennant, T. (1777). *The British zoology* (Vol. 4, 4th ed.). Benjamin White. <https://www.biodiversitylibrary.org/item/127011>
- Petersen, S., & Anger, K. (1997). Chemical and physiological changes during the embryonic development of the spider crab, *Hyas araneus* L. (Decapoda: Majidae). *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology*, 117(2), 299–306. [https://doi.org/10.1016/S0305-0491\(97\)00091-6](https://doi.org/10.1016/S0305-0491(97)00091-6)
- Pettersen, A. K., White, C. R., & Marshall, D. J. (2015). Why does offspring size affect performance? Integrating metabolic scaling with life-history theory. *Proceedings of the Royal Society B: Biological Sciences*, 282(1819), 20151946. <https://doi.org/10.1098/rspb.2015.1946>
- Phillips, G. (1971). Incubation of the English prawn *Palaemon serratus*. *Journal of the Marine Biological Association of the United Kingdom*, 51(1), 43–48. <https://doi.org/10.1017/S002531540006433>
- R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Reeve, M. R. (1969a). *Laboratory culture of the prawn Palaemon serratus*. H.M. Stationery Office.
- Reeve, M. R. (1969b). Growth, metamorphosis and energy conversion in the larvae of the prawn, *Palaemon serratus*. *Journal of the Marine Biological Association of the United Kingdom*, 49(1), 77–96. <https://doi.org/10.1017/S0025315400046427>
- Richard, P. (1974). *Contribution à l'étude du développement larvaire et de l'organogénèse chez Palaemon serratus, et du métabolisme des acides aminés libres chez cette espèce et chez Penaeus kerathurus*. Universitext d'Aix-Marseille.
- Richard, P. (1978). Tolérance aux températures extrêmes de *Palaemon serratus* (Pennant): Influence de la taille et de l'acclimatation. *Journal of Experimental Marine Biology and Ecology*, 35(2), 137–146. [https://doi.org/10.1016/0022-0981\(78\)90072-2](https://doi.org/10.1016/0022-0981(78)90072-2)
- Sá, R., Bexiga, C., Veiga, P., Vieira, L., & Erzini, K. (2006). Feeding ecology and trophic relationships of fish species in the lower Guadiana River Estuary and Castro Marim e Vila Real de Santo António Salt Marsh. *Estuarine, Coastal and Shelf Science*, 70(1), 19–26. <https://doi.org/10.1016/j.ecss.2006.05.038>
- Shirley, S. M., Shirley, T. C., & Rice, S. D. (1987). Latitudinal variation in the Dungeness crab, *Cancer magister*: Zoeal morphology explained by incubation temperature. *Marine Biology*, 95(3), 371–376. <https://doi.org/10.1007/BF00409567>
- Smith, G. G., Ritar, A. J., Thompson, P. A., Dunstan, G. A., & Brown, M. R. (2002). The effect of embryo incubation temperature on indicators of larval viability in Stage I phyllosoma of the spiny lobster, *Jasus edwardsii*. *Aquaculture*, 209(1), 157–167. [https://doi.org/10.1016/S0044-8486\(01\)00758-X](https://doi.org/10.1016/S0044-8486(01)00758-X)
- Sturbois, A., Cozic, A., Schaal, G., Desroy, N., Riera, P., Le Pape, O., Le Mao, P., Ponsoero, A., & Carpentier, A. (2022). Stomach content and stable isotope analyses provide complementary insights into the trophic ecology of coastal temperate benthodemersal assemblages under environmental and anthropogenic pressures. *Marine Environmental Research*, 182, 105770. <https://doi.org/10.1016/j.marenvres.2022.105770>
- Thatje, S., & Bacardit, R. (2000). Morphological variability in larval stages of *Nauticaris magellanica* (A. Milne Edwards, 1891) (Decapoda: Caridea: Hippolytidae) from South American waters. *Bulletin of Marine Science*, 66(2), 375–398.
- Tills, O., Holmes, L. A., Quinn, E., Everett, T., Truebano, M., & Spicer, J. I. (2022). Phenomics enables measurement of complex responses of developing animals to global environmental drivers. *Science of the Total Environment*, 858, 159555. <https://doi.org/10.1016/j.scitotenv.2022.159555>
- Torres, G., Thomas, D. N., Whiteley, N. M., Wilcockson, D., & Giménez, L. (2020). Maternal and cohort effects modulate offspring responses to multiple stressors. *Proceedings of the Royal Society B: Biological Sciences*, 287(1929), 20200492. <https://doi.org/10.1098/rspb.2020.0492>
- Tropea, C., Stumpf, L., & Greco, L. S. L. (2015). Effect of temperature on biochemical composition, growth and reproduction of the ornamental red cherry shrimp *Neocaridina heteropoda heteropoda* (Decapoda, Caridea). *PLoS One*, 10(3), e0119468. <https://doi.org/10.1371/journal.pone.0119468>
- Udekem D'acoz, C. (1999). Inventaire et distribution des crustacés décapodes de l'Atlantique nord-oriental, de la Méditerranée et des eaux continentales adjacentes au nord de 25° N. *Collection des Patrimoines Naturels*, 40, 1–383.
- Urzúa, Á., Paschke, K., Gebauer, P., & Anger, K. (2012). Seasonal and interannual variations in size, biomass and chemical composition of the eggs of North Sea shrimp, *Crangon crangon* (Decapoda: Caridea). *Marine Biology*, 159(3), 583–599. <https://doi.org/10.1007/s00227-011-1837-x>
- Vázquez, M. G., Ituarte, R. B., Bas, C. C., & Spivak, E. D. (2013). Effects of temperature and salinity on the ovarian cycle and the embryonic development of the invasive shrimp *Palaemon macrodactylus*. *Journal of Crustacean Biology*, 33(2), 218–223. <https://doi.org/10.1163/1937240X-00002128>
- Wear, R. G. (1974). Incubation in British Decapod Crustacea, and the effects of temperature on the rate and success of embryonic development. *Journal of the Marine Biological Association of the United Kingdom*, 54(3), 745–762. <https://doi.org/10.1017/S0025315400022918>

- Wehrtmann, I. S., & Kattner, G. (1998). Changes in volume, biomass, and fatty acids of developing eggs in *Nauticaris magellanica* (Decapoda: Caridea): A latitudinal comparison. *Journal of Crustacean Biology*, 18(3), 413–422. <https://doi.org/10.1163/193724098X00241>
- Wehrtmann, I. S., & López, G. A. (2003). Effects of temperature on the embryonic development and hatchling size of *Betaeus emarginatus* (Decapoda: Caridea: Alpheidae). *Journal of Natural History*, 37(18), 2165–2178. <https://doi.org/10.1080/00222930210133291>
- Weiss, M., Thatje, S., & Heilmayer, O. (2010). Temperature effects on zoeal morphometric traits and intraspecific variability in the hairy crab *Cancer setosus* across latitude. *Helgoland Marine Research*, 64(2), 125–133. <https://doi.org/10.1007/s10152-009-0173-8>
- Yagi, H., & Ceccaldi, H. J. (1985). The role of temperature and salinity on moult, metamorphosis and growth at each larval

stage of *Palaemon serratus* (Pennant) (Crustacea, Decapoda, Palaemonidae). *Annales de l'Institut Océanographique, Paris (Nouvelle Série)*, 61(1), 75–93.

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