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Authors contributions

JBB Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, review & editing, Visualization. **BX** Conceptualization, Methodology, Validation, Writing - review & editing, Supervision, Funding acquisition. **AD** Methodology, Investigation, Writing - review & editing. **AP** Investigation. **EM** Investigation. **FLF** Supervision. **RC** Conceptualization, Methodology, Validation, Formal analysis, Data curation, Writing - review & editing, Supervision, Project administration, Funding acquisition.

Title: Temperature-mediated developmental plasticity in winter and summer larvae of *Palaemon serratus*

Authors: Jean-Baptiste Baudet¹, Benoît Xuereb¹, Aurélie Duflot¹, Agnès Poret¹, Emeline Maniez¹, Frank Le Foll¹, Romain Coulaud^{1*}.

¹Le Havre Normandie University (ULHN), FR CNRS 3730 SCALE, UMR-INERIS 02 Environmental Stresses and Biomonitoring of Aquatic Ecosystems (SEBIO), 25 rue Philippe Le Bon - 76600 Le Havre – France.

*Corresponding authors: romain.coulaud@univ-lehavre.fr

Abstract

In a seasonal environment, variation in larval phenotype and developmental plasticity allow crustacean larvae to maximise survival by lengthening or shortening their development. The aim of this study is to investigate the effects of temperature, laying season and their interaction on larval developmental pathways (larval instars and larval stages). We monitored the different larval stages and calculated the number of larval instars reached during the development of winter and summer larvae of *Palaemon serratus* incubated at 12, 16 or 20°C. We observed a great variability in the larval development (6 to 13 larval instars and 6 to 11 larval stages). A higher temperature decreases the development time and the number of larval instars. At a given temperature, the development time of winter and summer larvae was not different. Two larval stages were considered supernumerary (zoea 4 and 6), as they were more frequent at low temperatures. At higher temperatures, some larvae started to develop pleopods as early as the third instar, larval stage which had never been described (named here zoea 3'). This phenomenon was more common in winter larvae than in summer larvae. These results provide new insights into the expression of developmental plasticity in decapod larvae.

26 **Key words:** Larval ecology, Plasticity, Developmental pathways, Larval instars, Larval
27 stages, *Palaemon serratus*.

1. Introduction

Ecological Developmental Biology (Eco-Devo) approaches focus on the interactions between organisms and their environment, and their ability to optimise their growth and development (Gilbert, 2001). For Eco-Devo studies, marine decapod crustaceans represent interesting biological models because their complex life cycle is generally biphasic (for a review see Anger 2006), divided between a pelagic larval phase and a benthic adult life. Given the seasonal or spatial variability of the pelagic environment (*e.g.* food availability and quality, temperature), decapods may therefore exhibit a high degree of developmental plasticity (*i.e.* the capacity of a genotype to produce alternative developmental pathways; West-Eberhard 2003), allowing their larvae to cope with variable or even sub-optimal conditions (Anger, 2001). Several authors have studied the effects of environmental parameters on the larval development of marine decapods. Among abiotic parameters, temperature affects intermoult time, growth rate and number of larval moults achieved (Linck 1995, read in Giménez 2006; O'Connor *et al.* 2007; Oliphant *et al.* 2013). The amount of food ingested by the larvae determines the number of larval moult cycles and the rate of morphogenesis between them (Anger, 1987; González-Ortegón and Giménez, 2014). Thence, prolonged development has frequently been observed under poor zootechnical conditions (Críales and Anger, 1986; Giménez and Anger, 2003; González-Ortegón *et al.*, 2013; González-Ortegón and Giménez, 2014; Knowlton, 1974; Oliphant *et al.*, 2013; Ostrensky *et al.*, 1997). Conversely, abbreviated developments have been encountered under optimal conditions such as the thermal preference (Críales and Anger, 1986; Oliphant *et al.*, 2013; Oliphant and Thatje, 2013). It is these different plastic responses to environmental conditions that lead to different developmental pathways (Críales and Anger, 1986).

In other way, few authors have studied the interactions of environmental conditions and the offspring phenotype on the developmental plasticity of decapods (Linck 1995, read in Giménez 2006; Hancock 1998; Oliphant & Thatje 2013; González-Ortegón & Giménez 2014; Oliphant

et al. 2014). The larval size is highly correlated with the nutritional reserves transferred per egg by the females during oogenesis (Giménez and Anger, 2001; Giménez and Torres, 2002; Hancock, 1998; Moland *et al.*, 2010). This increases their fitness by allowing them to better resist starvation and achieve a shorter development (Giménez *et al.*, 2004; Giménez and Anger, 2003; González-Ortegón and Giménez, 2014; Hancock, 1998; Oliphant *et al.*, 2014; Oliphant and Thatje, 2013). The larval phenotype is therefore determined by maternal investment, in line with environmental variations. The largest larvae correspond to the most difficult environmental conditions, such as the beginning of the season (González-Ortegón *et al.*, 2018; Paschke, 1998; Paschke *et al.*, 2004; Urzúa and Anger, 2013). Thus, decapods living in seasonally variable environments and reproducing several times during the year show a seasonal pattern in the “fertility x offspring size trade-off” (Bas *et al.*, 2007; Boddeke, 1982; Vázquez *et al.*, 2013). The developmental pathways of the larvae of these species should be seasonally different, linked to the difference in larval size between the seasons.

The larval developmental pathway is therefore the result of the interaction between larval genotype, environmental conditions during development and the environment or phenotype of the mother (*i.e.* maternal effects, Marshall *et al.*, 2008). In order to study the developmental plasticity response to this interaction, it is necessary to define the developmental pathways taken. Decapod larvae develop through a succession of moults with morphological, ecological and behavioural changes, which are generally called “Larval Stages” (Anger, 2001). However, in caridean shrimps that develop anamorphically in particular (*i.e.* through a gradual pattern of development, Møller *et al.* 2020), the degree of morphological changes between moults is variable (Anger, 2001; for a review see Quinn, 2016). Additional larval stages may be “intercalated” into the developmental sequence, often called “supernumerary stages”, displaying intermediate morphology (Knowlton, 1974; Little, 1969). Each larval stage can also be “repeated”, without showing any significant change (Rothlisberg, 1980; Walsh, 1993;

Wehrtmann and Albornoz, 1998). We thus explain that the larvae of a species do not necessarily develop through a fixed number of moults. Therefore, the neutral term "Larval Instar" is preferred to refer to the successive moult cycles during larval development, without describing them (Martin et al., 2014; Phillips and Sastry, 1980).

It seems necessary to describe the number of larval instars reached and the different successive larval stages to accurately characterise the larval developmental pathway. Some authors have study the developmental plasticity of caridean shrimp larvae in response to environmental factors by focusing on larval stages, larval instars or both. Hancock (1998) described the larval stages of *Paratya australiensis* encountered during development at 2 temperatures. Oliphant *et al.* (2014) counted the number of larval instars achieved by *Palaemonetes varians* in relation to food availability. González-Ortegón and Giménez (2014) carried out the same type of experiment on *P. serratus* larvae adding the effects of temperature and salinity. Oliphant *et al.* (2013) monitored both the larval stages and larval instars of *P. varians* during development at 3 temperatures. Críales and Anger (1986) described the developmental pathways (larval stages and instars) of *Crangon crangon* and *C. allmanni* according to rearing temperature. Linck (1995, read in Giménez, 2006) is the only author to have studied the effects of the interaction between temperature and laying season on larval development pathways (*C. crangon*).

To investigate the effects of the interaction between temperature and seasonal variations in larval size on the variability of larval developmental pathways, we chose to work with the caridean shrimp, *Palaemon serratus* (Pennant, 1777). This species is abundant in European coastal environments and has a life span of 3 to 5 years (Campillo, 1979). Its reproductive cycle consists of two annual clutches (commonly called "winter laying" and "summer laying"), characterised by larger eggs, and thus larvae, in the first clutch (Campillo, 1979; González-Ortegón et al., 2018). This species is known to carry out larval development with a variable number of instars; mostly 6 to 9 but ranging from 6 to 22 in the laboratory (Campillo, 1979;

Fincham and Figueras, 1986; Kelly et al., 2012; Reeve, 1969a). This developmental plasticity is mainly temperature-mediated, with the larvae of this species performing fewer instars in warm water than in cold water (González-Ortegón and Giménez, 2014). However, variations in developmental pathways due to temperature-mediated plasticity have not been investigated in *P. serratus* (larval stages and instars). The effects of seasonal variation in the size of the larvae of this species on their development have also not been studied, although this should also influence their developmental pathways (González-Ortegón et al., 2018). We hypothesise the following two scenarios. Large winter larvae develop faster than small summer larvae at the same temperature, completing fewer larval instars. Furthermore, the interaction between temperature and laying season has synergistic effects on developmental pathways. To test these hypotheses, we monitor the different stages and calculate the number of instars reached during the development of larvae from winter and summer females of *P. serratus* incubated at 3 temperatures, 12, 16 and 20°C.

2. Material and methods

2.1 Collection and maintenance of females

To study the larval development of the winter and summer laying, ovigerous *P. serratus* females (6 per seasons ; Fig.1) were respectively sampled between 29/04/2021 and 12/05/2021, and between 23/06/2021 and 28/06/2021 by hand-netting on Saint-Jouin-Bruneval foreshore (Seine-Maritime, France). Only the specimens carrying eggs at the end of development were selected for the study. The length of the cephalothorax was constant for both seasons, measured respectively 40.8 mm (± 1) for winter females and 39.8 mm (± 1.1) for summer females, in mean (\pm S.E.). The shrimps were transferred to the laboratory of the University of Le Havre (Seine-Maritime, France), and then maintained under photoperiod 12: 12 (L: D) in 100 L tank

temperature-controlled at 16°C, filled with filtered aerated natural seawater at 30 ppt (± 4) of salinity (Fig. 1). Seawater was renewed by half 3 times per week to avoid nitrate increase. Each specimen was isolated in wire baskets covered with fine mesh and fed individually twice a week *ad libitum* with pieces of squid. Larval hatching was checked daily.

2.2 Larval maintenance

The objective was to incubate larvae from 12 clutches (6 winter and 6 summer) at three temperature treatments of 12, 16 and 20°C, as shown in Figure 1. On hatching, actively swimming larvae were separated from females using a pipette. The rostro-telson length of 30 newly hatched larvae from each clutch was measured (Campillo, 1979). For each clutch, 3 groups of 104 larvae were distributed in three conical vessels, with filtered seawater at 30 ppt of salinity (± 4), at a density of 100 larvae per L (Reeve, 1969b; Torres et al., 2021). The water was initially at the same temperature as for the maintenance of the females, and then the conical vessels were distributed to 3 incubators (temperature $\pm 0.3^\circ\text{C}$, regulated by a TK700 cooling unit by TECO), with photoperiod 12: 12 (L: D) and constant thin aeration. This resulted in a gradual change which allowed time for the larvae to acclimate to the new temperatures (Richard, 1978). Larvae were fed daily with freshly-hatched *Artemia sp.* nauplii at a density of 10 nauplii per mL (Reeve, 1969b). The water was changed (100 %), and larval mortality and development, assessed by identification of stages (see section 2.4), were monitored 3 times a week. During development, the oxygen saturation was 103 % (± 4), the pH was 8 (± 0.1) and the ammonium concentration was 1 mg per L (± 0.3), in mean (\pm S.E.). On moulting to the juvenile stage, shrimps were removed.

2.3 Intermoult time and number of instars

As several successive stages can occur without morphological change, it is necessary to determine the number of larval instars. Because the larvae are mass-reared, the larval average intermoult time cannot be individually measured and then need to be calculated. The average intermoult time of *P. serratus* larvae is known to be constant in good zootechnical conditions (González-Ortegón and Giménez, 2014; Reeve, 1969a). We compiled data on the duration of larval development of *P. serratus* under controlled temperature conditions available in the literature. We did not use data concerning larvae exposed to other stresses (salinity, contaminant, ...). This allows the construction of a function expressing the theoretical intermoult time of larval as a function of temperature. For each juvenile obtained in the experiment, its number of instars realised is estimated by dividing its developmental time by the corresponding theoretical intermoult time.

2.4 Identification of larval stages

The different larval stages are identified using morphological criteria. In the larvae of European palaemonidae, the morphological criteria corresponding to the rostrum, caudal region and pleopods are commonly used to identify the different larval stages (Fincham and Figueras, 1986). Fincham and Figueras (1986) described 9 larval stages for *P. serratus*, while Campillo (1979) described 6. Description and terminology for the naming of larval stages differ between these authors, but it is possible to do correspondences and characterise 10 different larval stages (Table 1; according to Duflot et al., unpublished). According to these authors, these larval stages are potentially all observable, but are not obligatory stages through which each larvae must pass to develop. On the recent recommendations of Møller *et al.* (2020) regarding the terminology of caridean shrimp larvae, we call these stages zoea 1 to zoea 10 in chronological order of morphogenesis.

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176 Table 1: Correspondences between the nomenclatures of the larval stages of *Palaemon serratus*
 177 described Campillo (1979), Fincham & Figueras (1986) and us; according to Duflot et al.,
 178 unpublished. The morphological criteria used in this study are outlined.

Authors	Zoea								Juvenile		
Campillo (1979)	1	2	3		4		5	6			
Fincham and Figueras (1986)	1	2	3	4	5	6	7	8	9		
Correspondences	1	2	3	4	5	6	7	8	10		
Morphological criteria	Sessile eyes	Pedunculated eyes, 1 rostral spine	2 rostral spines	3 rostral spines, telson trapezoidal shape, no pleopod buds	3 rostral spines, telson trapezoidal shape, little pleopod buds	Telson rectangular shape, little pleopod buds	Telson rectangular shape, rudimentary pleopod buds	Rudimentary biramous pleopods	Well-developed pleopods, endopod of antenna 2 not longer than exopod by more than 2 segments	3 rostral curved spines, endopod of antenna 2 longer than exopod (≥ 2 segments)	Toothed rostrum (> 6 dorsal teeth)

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2.5 Statistical analysis

Statistical procedures were implemented with R software (R Core Team, 2020). The relationship between larval intermoult time and temperature (Fig. 3; Eq. 1) was obtained using the *nls* function. The difference in larval size between winter and summer laying was tested using a nonparametric Wilcoxon Rank Sum test. To test the effects of temperature and laying season on the rate of larval metamorphosis and the development time of the metamorphosed larvae, we used mixed-effects models to consider the fact that for each of the seasons, the larvae used in the different temperatures came from the same females. For the rate of larval metamorphosis, we fitted generalised linear mixed-effects model with a logit link function and a binomial error distribution (*glmer* function of the package *lme4*) and performed deviance analysis procedure including interaction terms (using the package *car*). For the development time of the metamorphosed larvae, we fitted linear mixed-effects model (using the function *lmer* of the package *lme4*) and performed deviance analysis procedure including interaction terms (using the package *car*).

3. Results

3.1 Zootechnical performances during larval development.

The average total length of hatching larvae was significantly higher in winter (3.68 ± 0.07 mm), than in summer (3.18 ± 0.05 mm) in mean \pm S.E. (Wilcoxon Rank Sum test; $p < 0.05$).

While all females produced juveniles at 16 and 20°C, only 5 winter and 3 summer females produced juveniles at 12°C. At 12°C, only 18 of the 624 winter larvae and 5 of the 624 summer larvae metamorphosed (Fig. 2a). At 16 and 20°C respectively, 30 % (± 5) and 41 % (± 7) of the winter larvae metamorphosed, compared to 43 % (± 7) and 55 % (± 7) of the summer larvae, in mean (\pm S.E.). The rate of larval metamorphosis varied significantly with temperature and

laying season without interaction of these two factors (Deviance analysis, interaction term: $Chisq = 3.18$, $p = 0.07$; temperature: $Chisq = 16.19$, $p < 10^{-5}$; season: $Chisq = 26.6$, $p < 10^{-7}$; $n = 6$ per temperature and season).

The metamorphoses took place between days 65 and 111 at 12°C, between days 30 and 56 at 16°C and between days 19 and 42 at 20°C (Fig. 2b). The development time of the metamorphosed larvae varied significantly between the three incubation temperatures, but neither as a function of the laying season nor as a result of the interaction of these two factors (Deviance analysis, interaction term: $Chisq = 0.76$, $p = 0.4$; temperature: $Chisq = 138.73$, $p < 10^{-16}$; season: $Chisq = 0.62$, $p = 0.43$; $n = 6$ per temperature and season).

3.2 Number of instars achieved by larvae.

The compilation of literature data on the larval development of *P. serratus* under controlled temperature conditions allows us to construct a function expressing the theoretical larval intermoult time *versus* temperature (Fig. 3; Eq. 1):

$$LIT = 147.96 e^{(-0.25 \text{ temp})} + 2.45 \quad \text{Eq. 1}$$

where *LIT* is the theoretical larval intermoult time and *temp* the incubation temperature.

This function allows us to calculate the theoretical intermoult times at 12°C (9.8 days), 16°C (5.2 days) and 20°C (3.4 days) as well as the number of instars achieved by each juvenile obtained in this experiment. In all experimental conditions, the larvae that metamorphosed did so after 6 to 13 larval instars (Fig. 4). Only about 3.7 % of them developed for more than 9 instars, and about 1 % for 6 instars. While about 33 and 45 % of the larvae performed 7 instars at 16 and 20°C, about 43 and 31 % of them performed 8 instars. At 20°C, larvae metamorphosing after 7 instars represented about 40 % of the total in winter and 50 % in

summer. At 16°C, 3 larvae metamorphosed after 6 instars in summer, while none did so in winter.

3.3 Succession of larval stages.

Figures 5 to 7 show the number of individuals observed for each larval stage during development, separating the larvae by clutch and incubation temperature. With the exception of the first few days of development, the larvae from the same clutch incubated at the same temperature showed a diversity of larval stages, highlighting different developmental pathways within the same clutch. This diversity increased during development, so that the time of observation of a larval stage within the clutch also increased during monitoring. Regardless of the experimental conditions and the rate of metamorphosis, larval mortality is constant throughout development. Only the larvae of the females 2, 4 and 9 at 12°C experienced more than 50 % mortality from the zoea 1 stage (Fig. 5).

All 10 larval stages described were observed at each temperature. However, we observed differences in the proportions of the different larval stages. At 12, 16 and 20°C, respectively, at least 15.3, 5.9 and 0.4 % of the larvae passed through the zoea 4 stage, and at least 9.1, 0.6 and 0.3 % of the larvae passed through the zoea 6 stage.

Furthermore, during the monitoring of the larval stages presented here, we frequently observed larvae with 2 rostral spines (criteria for zoea 3) and pleopod buds (criteria for zoea 5). This larval stage seems to take place instead of the zoea 3 stage, so we called it zoea 3'. This never described larval stage was not observed at 12°C. At 16 and 20°C, respectively, at least 58.1 and 67.8 % of the winter larvae passed through the zoea 3' stage, compared to at least 20.8 and 19.9 % of summer larvae.

4. Discussion

Regardless of the incubation temperature and the laying season from which the larvae hatched, we observed a great variability in the larval development of *P. serratus* (6 to 13 larval instars and 6 to 11 larval stages). The different developmental pathways observed underline the developmental plasticity of this species.

In contrast to several authors studying the number of larval instars of decapods during development (Reeve, 1969a; Dalley, 1980; Linck, 1995, read in Giménez, 2006), we did not rear the larvae individually. This choice was made in view of the survival rates of *P. serratus* larvae in the laboratory available in the literature. While González-Ortegón and Giménez (2014) and Lassus and Maggi (1980) achieved respectively 40 and 45-70% metamorphosis when rearing larvae individually, Campillo (1979) and Reeve (1969b) achieved respectively 76 and over 90% metamorphosis with mass-rearing. Furthermore, Reeve (1969a) observed longer larval development with lower survival when rearing *P. serratus* individually than when mass-rearing.

We calculated the number of instars made by the larvae from their average intermoult time according to bibliographic data. Intermoult times obtained for the same temperature may vary slightly between the 6 sources used (Fig. 3). This can be explained by the differences in experimental protocol and by maternal effects. The limited information available on this second factor complicates discussions on this subject. The females used in these 6 experiments came from populations in Ireland, Wales, Brittany and the Mediterranean (the latter being phylogenetically distant from the Atlantic populations; Weiss et al., 2018). Only González-Ortegón and Giménez (2014) specify the period of collection of females (autumn) as well as their size (between 17 and 24 mm from the postorbital margin to the end of carapace, between 18 and 22 mm in our study). According to Reeve (1969a) and González-Ortegón and Giménez (2014), the intermoult time of *P. serratus* is constant during larval development under good

zootechnical conditions. Nevertheless, these authors reared the larvae of this species between 18 and 24°C. It is possible that the intermoult time of *P. serratus* larvae increases as development proceeds at lower temperatures, as reported by Kelly et al. (2012) and Lassus and Maggi (1980) between 10 and 13°C. However, the few individuals that metamorphosed at 12°C leads us to put the interpretation of the number of instars carried out at this temperature into perspective.

4.1 Temperature-mediated developmental plasticity

The larval development of *P. serratus* is temperature-driven. Here, metamorphosis rates were temperature dependent (about 2, 36 and 49 % at 12, 16 and 20°C respectively). Campillo (1979) experienced the highest rates of metamorphosis (85 %) by incubating *P. serratus* larvae from Roscoff (France) at 27°C, a temperature above the local maximum. Other authors who studied the larval development of *P. serratus* at temperatures between 10 and 13°C observed a mortality of all individuals between the third and fourth larval instar (Kelly et al., 2012; Lassus and Maggi, 1980; Yagi and Ceccaldi, 1985). We also observed very low survival rates at 12°C, but we managed to get some individuals to metamorphosis (< 2%) after 7-13 instars. We chose to incubate larvae at 12°C because this is the temperature of the sea water in the Bay of Seine (Normandy) at the beginning of May (Claquin et al., 2018), the date at which the larvae from the winter spawning are released by females of the same size as those used for this study (personal observations). Mortality at 12°C was constant during development in the laboratory. At this temperature, only the larvae from 3 of the 12 females suffered mortality rates above 50 % by the end of the first instar. The mortality rate of the larvae was approximately 52 % after 30 days of incubation, when most of them were in their fourth instar. The thermal optimum of crustacean larvae experiences an ontogenic shift (Sastry and McCarthy, 1973). These variations between larval stages are due to temperature-induced changes in metabolic rates

(Small et al., 2015). During the month of May, the temperature of the sea water in the Bay of Seine increases by approximately 3°C (Claquin et al., 2018). A constant temperature of 12°C in the laboratory negatively affects the survival rates of *P. serratus* larvae. These effects probably increase during ontogeny.

In addition to decreasing survival, colder water increases the duration of development. First of all, as we know from the literature, the intermoult time increases as the temperature decreases following a negative exponential relationship (Fig. 2). Secondly, larvae tend to go through a greater number of instars in colder waters (Fig. 4). Although the duration of development is variable between individuals incubated at the same temperature, this is not so with the value of the average duration per family (Fig. S1, Supplement). The plastic response to temperature therefore appears to be the same for larvae produced by different females. However, differences in survival rates appear between larvae of different families (Fig. S1, Supplement).

Concerning the larval stages, zoea 4 and zoea 6 are more frequent in colder water (Fig. 5 to 7). These larval stages can be interpreted as supernumerary, or intercalated, stages occurring under unfavourable conditions such as low temperature. This would explain why Campillo (1979) did not describe them at 27°C (Table 1). Conversely, at 16 and 20°C, many larvae with zoea 3 criteria (2 rostral spines) and zoea 5 criteria (pleopod buds) were observed (about 39 and 44 % at 16 and 20°C respectively). This never described stage, which we have called zoea 3', seems to replace the zoea 3 stage. This larval stage can be interpreted as a sign of abbreviated development, occurring under favourable conditions. Caridean shrimps have anamorphic development, with gradual morphogenesis. Several authors attempt to define and differentiate terminologies such as repeated instars, supernumerary and intermediate stages. These terms are the result of the conservative belief in immutable development in decapod crustaceans (Sandifer and Smith, 1979). The study of the anamorphic development of caridean shrimps allows us to consider this belief as a zombie idea. The multiple examples of developmental plasticity

observed in species from different groups of decapods support this view (for a review see Quinn, 2016).

As stated in the introduction, this temperature-mediated developmental plasticity has already been demonstrated in caridean shrimps. The larvae follow shorter developmental pathways in temperatures closer to their thermal optimum (Críales and Anger, 1986; Linck, 1995, read in Giménez, 2006; Oliphant et al., 2013). Generally, at a given temperature, the more instars the larvae develop through, the larger the juveniles. This trend has been demonstrated in the larvae of several decapods including *Chasmagnathus granulata* (Giménez and Torres, 2002) and *P. varians* (Oliphant et al., 2013). Therefore, it would be interesting to compare the consequences of temperature-mediated developmental plasticity of *P. serratus* larvae on the phenotype of juveniles.

These differences in survival between thermal conditions can also be explained by differences in nutritional requirements. Crustacean larvae require long-chain polyunsaturated fatty acids (PUFAs) for development, such as eicosapentaenoic acid, or EPA, and docosahexaenoic acid, or DHA (Anger, 1998; Bergé and Barnathan, 2005). These are generally synthesised by phytoplankton and transferred into the food chain (Lubzens et al., 1995). PUFAs, DHA in particular, maintain membrane integrity and viscosity (Estévez and Kanazawa, 1996; Los and Murata, 2004; Pagliarani et al., 1986), especially in cold waters (Harwood, 1988; Munro and Thomas, 2004). Like many authors, we fed *P. serratus* larvae with artemia nauplii (Campillo, 1979; Reeve, 1969b; Wickins, 1972; Yúfera and Rodríguez, 1985). Although these are traditionally used to feed decapod larvae, they are known to be deficient in PUFAs (Narciso and Morais, 2001; Navarro et al., 1999). These deficiencies may explain the very low survival of *P. serratus* larvae in cold water observed here and by the authors mentioned in the paragraph above. PUFAs also influence growth, stress and disease resistance in decapods (Anger, 1998; Kanazawa et al., 1985; Mourente and Rodríguez, 1997). It would be interesting to study the

effects of the interaction between temperature and diet quality on the developmental plasticity of *P. serratus*.

4.2 Developmental plasticity induced by laying season and its interaction with temperature

The newly hatched larvae used in this study were larger in winter than in summer. These results are consistent with González-Ortegón *et al.* (2018) who observed difference in *P. serratus* larval biomass between laying seasons. Because of this difference in phenotype, we hypothesised that *P. serratus* larvae from winter females would develop faster than those from summer females. These effects were not significant in our data analyses. At a given temperature, summer larvae even appeared to perform fewer larval instars than winter larvae. These results are in contradiction with those obtained on another caridean shrimp species (Linck, 1995, read in Giménez, 2006). The author incubated larvae of *C. crangon*, from large winter eggs and small summer eggs, at two relatively cold and warm temperatures (12 and 18°C). Regardless of the temperature, summer larvae metamorphosed after a greater number of larval instars than winter larvae. We need to further investigate the effects of the interaction between the laying season and environmental conditions on the developmental plasticity of *P. serratus*.

The winter larvae were larger than the summer ones. Few authors have studied the effects of larval size or larval biomass on developmental plasticity of decapod larvae. The number of larval instars made by larvae decreases with increasing larval size or larval biomass in *C. crangon* (Paschke *et al.*, 2004), *C. granulata* (Giménez *et al.*, 2004), *Homarus gammarus* (Moland *et al.*, 2010), *P. varians* (Oliphant *et al.*, 2014; Oliphant and Thatje, 2013) and *P. australiensis* (Hancock, 1998), a phenomenon that is accentuated under adverse conditions. Although they highlighted the decrease in the number of larval instars with increasing initial

larval biomass in *P. serratus* larvae under starvation conditions, González-Ortegón & Giménez (2014) did not confirm this trend under favourable feeding conditions. This result is consistent with those presented here.

Although the development time of the larvae in the two laying seasons did not differ, at 16 and 20°C, the zoea 3' stage was observed more often in winter larvae than in summer larvae (Fig. 5 to 7). The morphogenesis of the winter larvae (pleopod buds) was earlier than that of the summer larvae, at least in the early larval stages. The winter larvae may have received more available energy resources (transmitted by the mother) than summer larvae and used them during these early instars. This phenomenon may have been favoured by the choice of females used. The cephalothorax of the winter females measured on average about 40 mm. These would be more than two years old, which corresponds to less than 2 % of the female population of *P. serratus* (Campillo, 1979). The limited information available on the size of the females and the date of their sampling in previous publications does not allow comparison of our results. The lack of description of the zoea 3' stage in previous studies can be explained by the choice of females used. We need to investigate the effects of female age on maternal investment and developmental plasticity in *P. serratus*.

When they hatch, decapod larvae have visible vitelline reserves in the cephalothorax in the form of yolk droplets (Anger, 1996; Oliphant and Thatje, 2014). These can be used to cope with starvation conditions during the first larval instars (Anger, 1995a, 1995b; Thessalou-Legaki et al., 1999), *e.g.* when larvae are exported from a brackish environment to the marine environment (Anger and Hayd, 2009; Oliphant and Thatje, 2014). Such yolk droplets are observed in hatched larvae of *P. serratus* (personal observation). Narciso and Morais (2001) measured a decrease in fatty acid content during the first 48 hours of development of *P. serratus* larvae under starvation conditions. Their results and ours seem to confirm the use of vitelline reserves during the first larval instars in *P. serratus*. Future analyses to compare the quantity

and quality of resources allocated per offspring, called POI (*i.e.* per offspring investment; Oliphant, 2014), as a result of the laying season and their effects on larval development will provide a better understanding of the developmental plasticity in *P. serratus* larvae.

In *P. serratus*, winter larvae are larger than summer larvae. We expected that this phenotypic difference would allow winter larvae to develop faster than summer larvae at the same temperature. Although we did not observe this result, we did observe earlier morphogenesis in winter larvae at the warmest temperatures. As explained in the previous paragraphs (see section 4.2), we believe that this phenomenon is related to the amount of energy allocated per offspring. This pattern of maternal investment buffers winter larvae from variable early season conditions (low temperature, Torres et al., 2020; less abundant planktonic food resources, Paschke et al., 2004). Furthermore, the negative effects of food limitation on larval survival are exacerbated by unfavourable temperatures (Torres and Giménez, 2020). The few months separating the hatching of the larvae from the two laying periods of *P. serratus* result in two cohorts of juveniles (Campillo, 1979). As these cohorts share the same habitats, they compete for resources or even cannibalise (Moksnes et al., 1998). The shift in the recruitment periods of these two cohorts results in a difference in the size of the individuals (*P. serratus* juveniles of 0.5g which double or triple their weight in 2 months depending on their sex at temperatures between 18 and 29°C; Rodriguez, 1981). These traits probably favour juveniles from winter laying over those from summer laying in years when early season conditions are favourable (Temming et al., 2017). The population structure and dynamics of *P. serratus* should be studied to assess the settlement success of winter and summer cohort. This would facilitate understanding the effects of juvenile recruitment phenology on their interactions.

Conclusion

Although larval development of *P. serratus* is plastic in response to temperature, the interaction between temperature and laying season does not seem to influence its developmental pathways as expected. As the development of some groups of decapods is gradual, understanding their developmental pathways will require consideration of the number of instars and the succession of larval stages.

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Vitae

Jean-Baptiste Baudet is working on crustacean ecology, developmental plasticity, phenotypic links and larval ecology during his PhD project started in December 2020. His previous experience was in penaeid shrimp research and development.

Benoît Xuereb is a researcher at the research unit for Environmental Stresses and Biomonitoring of Aquatic Ecosystems laboratory (SEBIO), Le Havre – Normandy University. His research interest focuses on the description of ecophysiology and life traits in the palaemonid shrimps, with a perspective to propose reliable effect-based methods for ecotoxicological applications.

Aurélie Duflot works in the SEBIO laboratory on various fields related to the physiology of marine organisms and is an expert on the embryo-larval development of *Palaemon serratus*.

Agnès Poret is an engineer at the SEBIO laboratory working on marine invertebrates, especially on reproduction and immunology.

Emeline Maniez has completed a master's degree in marine sciences. She specialises in marine and fisheries ecology, as well as in the functioning and management of marine ecosystems. She is interested in shrimp and plankton, for example, in relation to global changes and/or fisheries.

Frank Le Foll is a professor of organismal biology at the University of Le Havre Normandie and currently the head of the Environmental Stresses and Biomonitoring of Aquatic Ecosystems laboratory (SEBIO). SEBIO carries out basic and translational research in bioenvironmental sciences and ecotoxicology. Frank research interest focuses on invertebrate immune cell activity, host-microbe-environment interactions, multitoxenobiotic resistance phenotype, immunomarker research and innovative cage design for biological monitoring of polluted water bodies.

Romain Coulaud is a researcher at the research unit for Environmental Stresses and Biomonitoring of Aquatic Ecosystems laboratory (SEBIO), Le Havre – Normandy University. His research interest focuses on the ecology, ecophysiology and ecotoxicology of macroinvertebrates (particularly crustaceans), using multi-scale approaches ranging from sub-

individual biomarkers to community functioning and combining laboratory and field experiments and modelling.

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Figure captions

Figure 1: Experimental design to study the effects of temperature and laying season on larval developmental pathways in *Palaemon serratus*. For the 12 females (6 per season), the larvae are distributed into conical vessels in 3 water baths following the illustrated example of the larvae of females 1 and 7. The illustrations of the females are modified from the one available on the Muséum-Aquarium de Nancy website by Marion Arbona.

Figure 2: (a) Metamorphosis rate (%) and (b) development time (days) of *Palaemon serratus* larvae having reached metamorphosis. The \pm S.E. correspond to the deviation of the mean of each family from the overall mean. Larvae are grouped by laying season and incubation temperature; W12: Winter 12°C, S12: Summer 12°C, W16: Winter 16°C, S16: Summer 16°C, W20: Winter 20°C and S20: Summer 20°C (n = 104 larvae per female).

Figure 3: Theoretical larval intermoult time of *Palaemon serratus* versus rearing temperature, based on data from bibliography (Reeve, 1969a, squares; Campillo, 1979, filled circles; Lassus & Maggi, 1980, cross; Yagi & Ceccaldi, 1985, stars; Kelly *et al.*, 2012, filled squares; González-Ortegón & Giménez, 2014, filled triangle).

Figure 4: The relative frequency (%) of the total number of larval instars reached by metamorphosed *Palaemon serratus* larvae. Larvae are grouped by laying season and incubation temperature; W12: Winter 12°C (n = 18), S12: Summer 12°C (n = 5), W16: Winter 16°C (n = 186), S16: Summer 16°C (n = 257), W20: Winter 20°C (n = 271) and S20: Summer 20°C (n = 350).

729

730 Figure 5: Number of *Palaemon serratus* larvae observed for each larval stage during their
731 development at 12°C. Larvae are grouped by clutch; 1 to 6: winter females, 7 to 12: summer
732 females (n = 104 larvae per female). Juveniles are removed at metamorphosis and their
733 cumulative numbers are shown in black on the graph. Observations stop when there are no more
734 larvae.

735

736 Figure 6: Number of *Palaemon serratus* larvae observed for each larval stage during their
737 development at 16°C. Larvae are grouped by clutch; 1 to 6: winter females, 7 to 12: summer
738 females (n = 104 larvae per female). Juveniles are removed at metamorphosis and their
739 cumulative numbers are shown in black on the graph. Observations stop when there are no more
740 larvae.

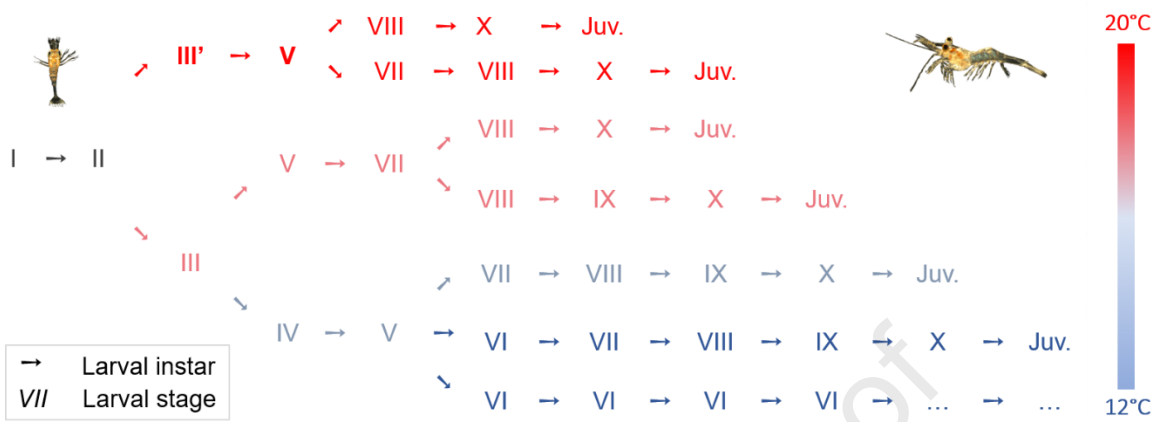
741

742 Figure 7: Number of *Palaemon serratus* larvae observed for each larval stage during their
743 development at 20°C. Larvae are grouped by clutch; 1 to 6: winter females, 7 to 12: summer
744 females (n = 104 larvae per female). Juveniles are removed at metamorphosis and their
745 cumulative numbers are shown in black on the graph. Observations stop when there are no more
746 larvae.

747

Graphical abstract

Most frequent developmental pathways in relation to temperature with winter and summer larvae



Figures

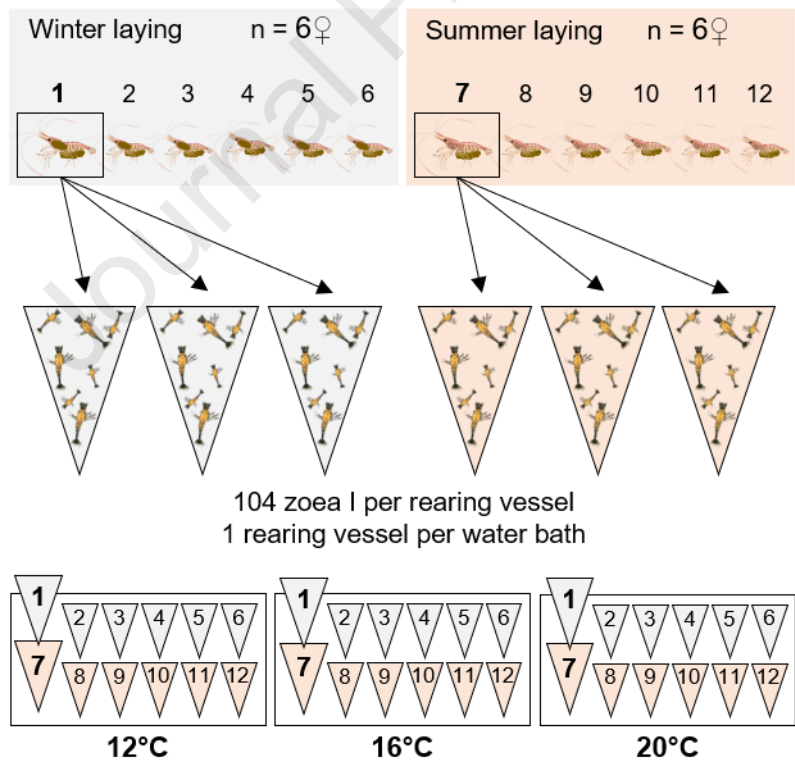


Figure 1

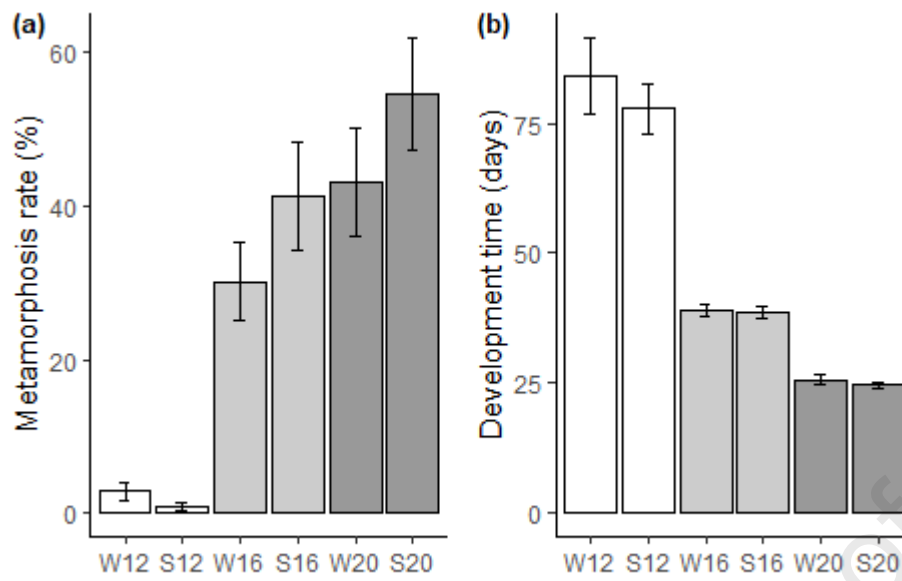


Figure 2

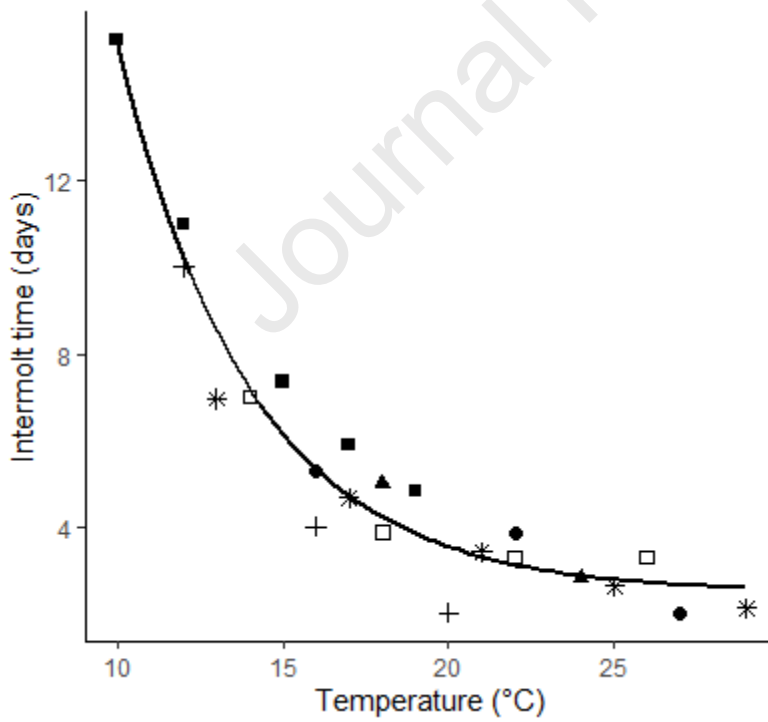
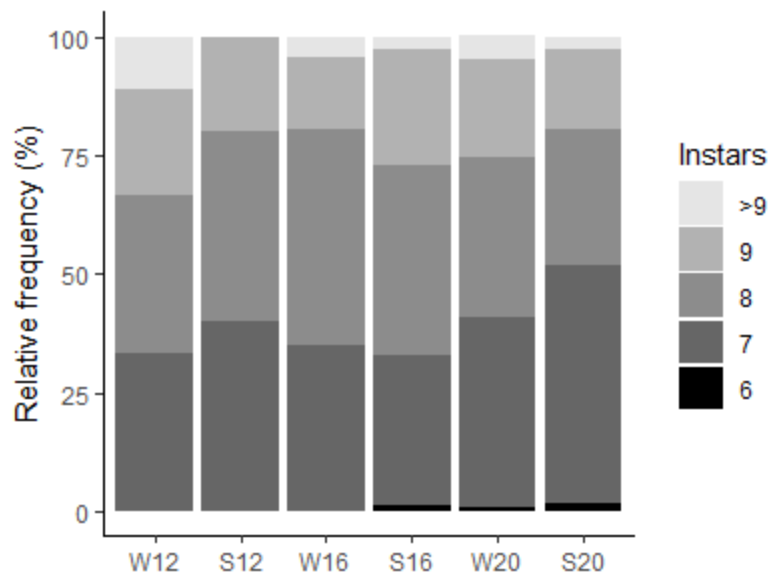


Figure 3



761

762 Figure 4

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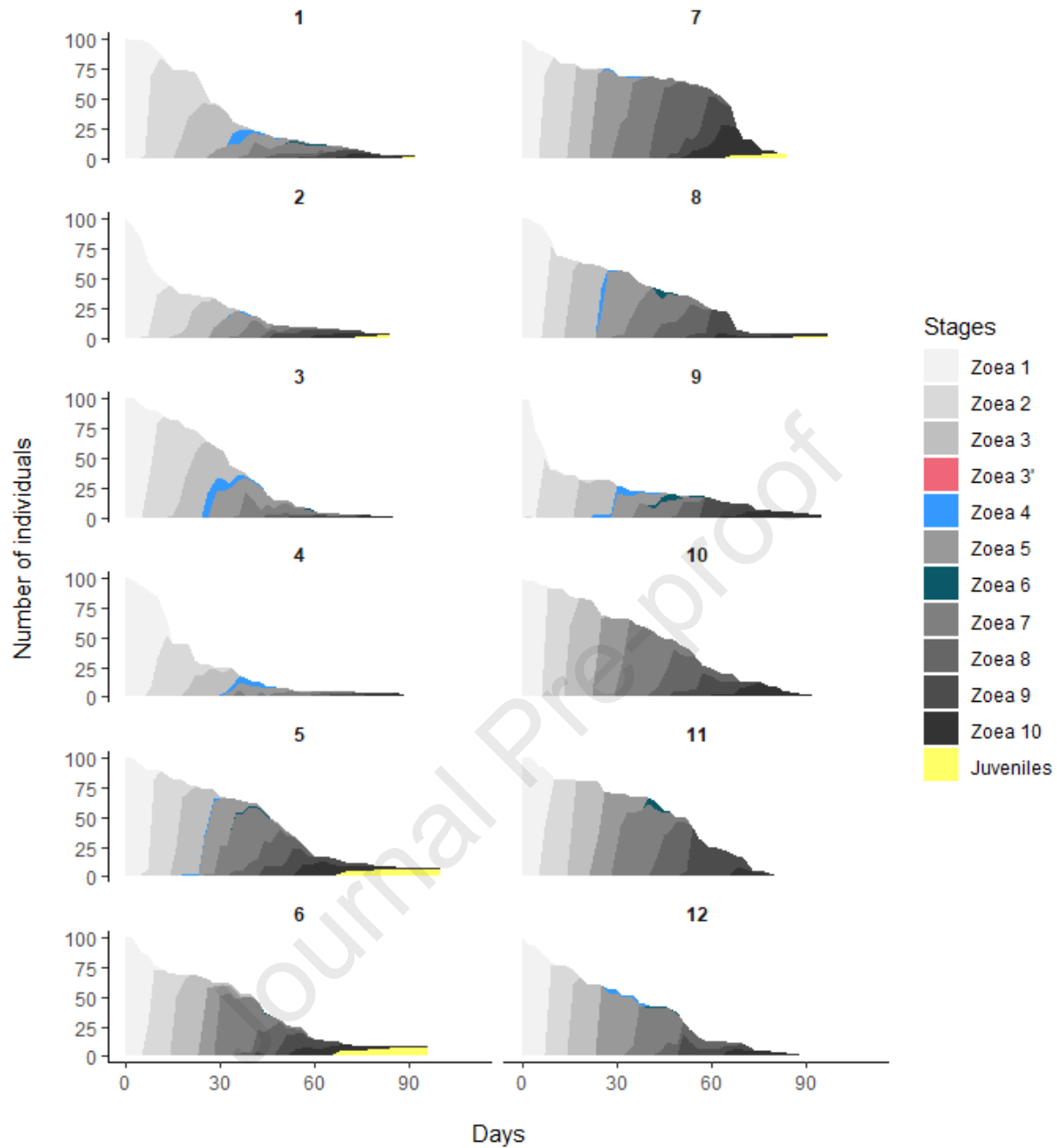


Figure 5

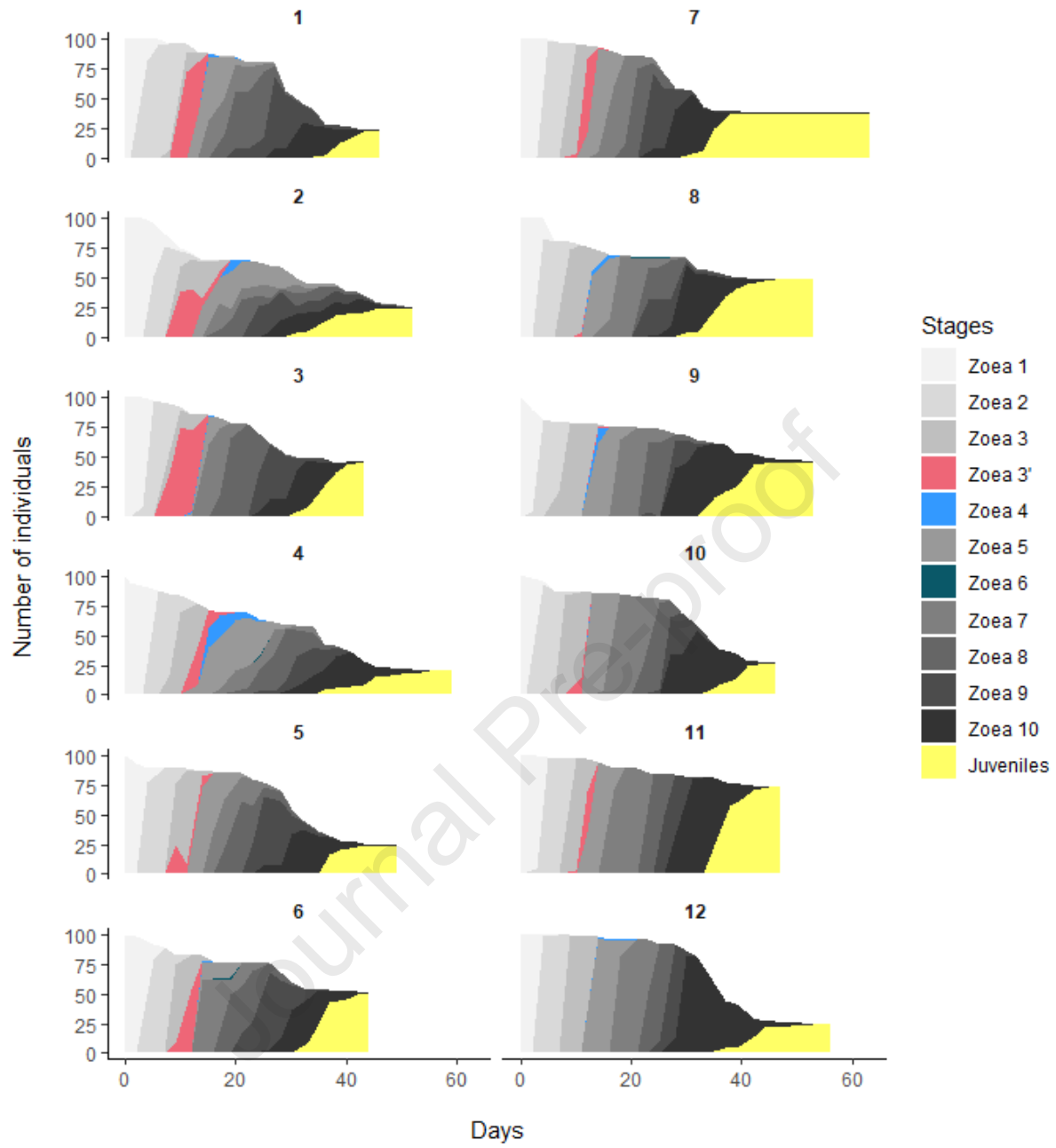


Figure 6

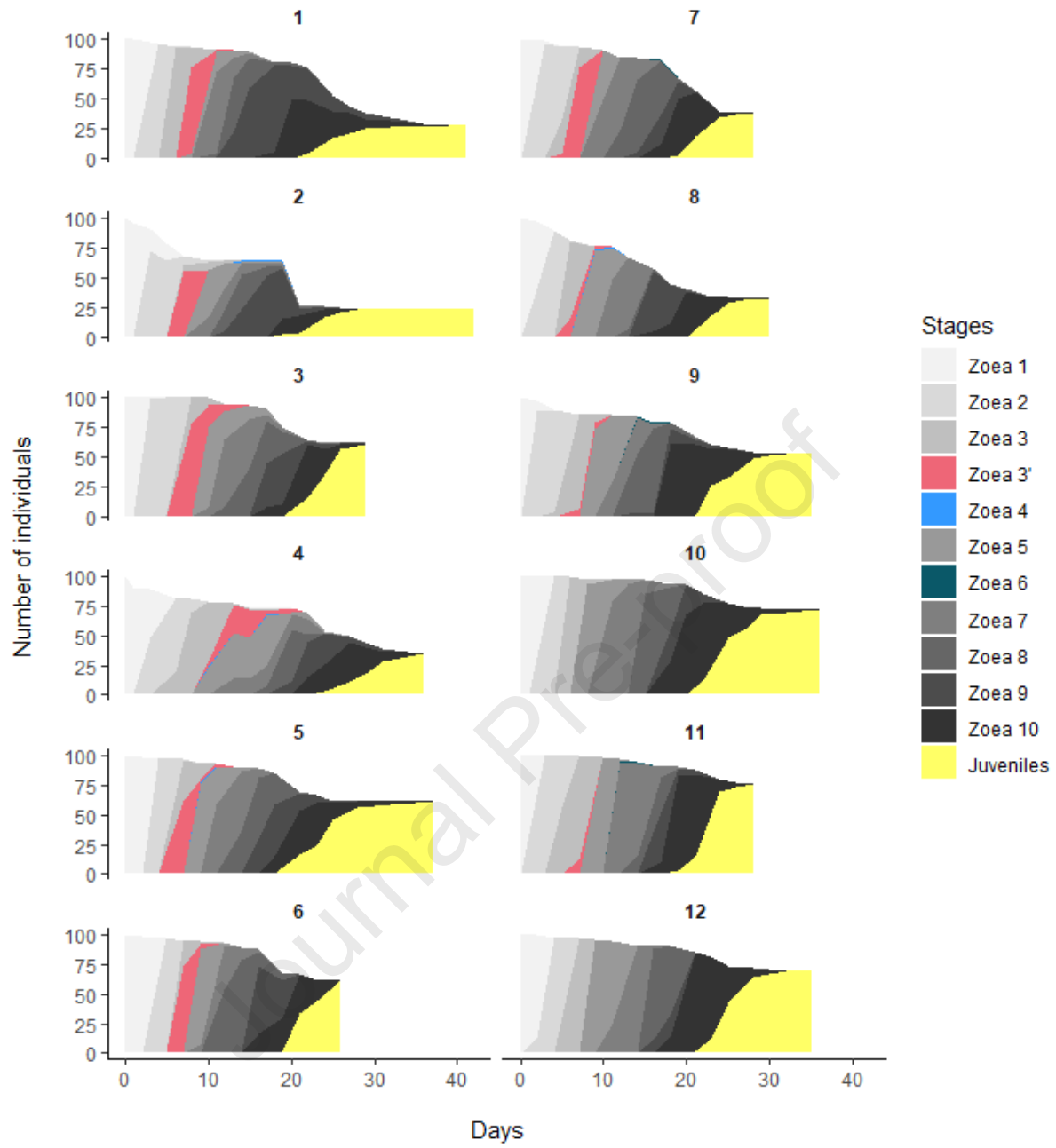


Figure 7

Highlights

- Larval development was plastic in terms of instars and stages.
- Higher temperature decreased the development time and the number of instars.
- The seasonal phenotype had no effect on the development time.
- Supernumerary stages were observed at low temperatures.
- Early morphogenesis was observed at high temperatures.

Declaration of competing interest

None.

Funding

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