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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.

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

3
4 **Authors:** Jean-Baptiste Baudet¹, Benoît Xuereb¹, Aurélie Duflot¹, Agnès Poret¹,
5 Emeline Maniez¹, Frank Le Foll¹, Romain Coulaud^{1*}.

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

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

10
11 **Abstract**

12 In a seasonal environment, variation in larval phenotype and developmental plasticity allow
13 crustacean larvae to maximise survival by lengthening or shortening their development. The
14 aim of this study is to investigate the effects of temperature, laying season and their interaction
15 on larval developmental pathways (larval instars and larval stages). We monitored the different
16 larval stages and calculated the number of larval instars reached during the development of
17 winter and summer larvae of *Palaemon serratus* incubated at 12, 16 or 20°C. We observed a
18 great variability in the larval development (6 to 13 larval instars and 6 to 11 larval stages). A
19 higher temperature decreases the development time and the number of larval instars. At a given
20 temperature, the development time of winter and summer larvae was not different. Two larval
21 stages were considered supernumerary (zoea 4 and 6), as they were more frequent at low
22 temperatures. At higher temperatures, some larvae started to develop pleopods as early as the
23 third instar, larval stage which had never been described (named here zoea 3'). This
24 phenomenon was more common in winter larvae than in summer larvae. These results provide
25 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*.

Journal Pre-proof

28 **1. Introduction**

29 Ecological Developmental Biology (Eco-Devo) approaches focus on the interactions between
30 organisms and their environment, and their ability to optimise their growth and development
31 (Gilbert, 2001). For Eco-Devo studies, marine decapod crustaceans represent interesting
32 biological models because their complex life cycle is generally biphasic (for a review see Anger
33 2006), divided between a pelagic larval phase and a benthic adult life. Given the seasonal or
34 spatial variability of the pelagic environment (*e.g.* food availability and quality, temperature),
35 decapods may therefore exhibit a high degree of developmental plasticity (*i.e.* the capacity of a
36 genotype to produce alternative developmental pathways; West-Eberhard 2003), allowing their
37 larvae to cope with variable or even sub-optimal conditions (Anger, 2001). Several authors have
38 studied the effects of environmental parameters on the larval development of marine decapods.
39 Among abiotic parameters, temperature affects intermoult time, growth rate and number of
40 larval moults achieved (Linck 1995, read in Giménez 2006; O'Connor *et al.* 2007; Oliphant *et*
41 *al.* 2013). The amount of food ingested by the larvae determines the number of larval moult
42 cycles and the rate of morphogenesis between them (Anger, 1987; González-Ortegón and
43 Giménez, 2014). Thence, prolonged development has frequently been observed under poor
44 zootechnical conditions (Críaes and Anger, 1986; Giménez and Anger, 2003; González-
45 Ortegón *et al.*, 2013; González-Ortegón and Giménez, 2014; Knowlton, 1974; Oliphant *et al.*,
46 2013; Ostrensky *et al.*, 1997). Conversely, abbreviated developments have been encountered
47 under optimal conditions such as the thermal preference (Críaes and Anger, 1986; Oliphant *et*
48 *al.*, 2013; Oliphant and Thatje, 2013). It is these different plastic responses to environmental
49 conditions that lead to different developmental pathways (Críaes and Anger, 1986).

50 In other way, few authors have studied the interactions of environmental conditions and the
51 offspring phenotype on the developmental plasticity of decapods (Linck 1995, read in Giménez
52 2006; Hancock 1998; Oliphant & Thatje 2013; González-Ortegón & Giménez 2014; Oliphant

53 *et al.* 2014). The larval size is highly correlated with the nutritional reserves transferred per egg
54 by the females during oogenesis (Giménez and Anger, 2001; Giménez and Torres, 2002;
55 Hancock, 1998; Moland *et al.*, 2010). This increases their fitness by allowing them to better
56 resist starvation and achieve a shorter development (Giménez *et al.*, 2004; Giménez and Anger,
57 2003; González-Ortegón and Giménez, 2014; Hancock, 1998; Oliphant *et al.*, 2014; Oliphant
58 and Thatje, 2013). The larval phenotype is therefore determined by maternal investment, in line
59 with environmental variations. The largest larvae correspond to the most difficult
60 environmental conditions, such as the beginning of the season (González-Ortegón *et al.*, 2018;
61 Paschke, 1998; Paschke *et al.*, 2004; Urzúa and Anger, 2013). Thus, decapods living in
62 seasonally variable environments and reproducing several times during the year show a
63 seasonal pattern in the “fertility x offspring size trade-off” (Bas *et al.*, 2007; Boddeke, 1982;
64 Vázquez *et al.*, 2013). The developmental pathways of the larvae of these species should be
65 seasonally different, linked to the difference in larval size between the seasons.

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

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

82 It seems necessary to describe the number of larval instars reached and the different successive
83 larval stages to accurately characterise the larval developmental pathway. Some authors have
84 study the developmental plasticity of caridean shrimp larvae in response to environmental
85 factors by focusing on larval stages, larval instars or both. Hancock (1998) described the larval
86 stages of *Paratya australiensis* encountered during development at 2 temperatures. Oliphant *et*
87 *al.* (2014) counted the number of larval instars achieved by *Palaemonetes varians* in relation to
88 food availability. González-Ortegón and Giménez (2014) carried out the same type of
89 experiment on *P. serratus* larvae adding the effects of temperature and salinity. Oliphant *et al.*
90 (2013) monitored both the larval stages and larval instars of *P. varians* during development at
91 3 temperatures. Críales and Anger (1986) described the developmental pathways (larval stages
92 and instars) of *Crangon crangon* and *C. allmanni* according to rearing temperature. Linck
93 (1995, read in Giménez, 2006) is the only author to have studied the effects of the interaction
94 between temperature and laying season on larval development pathways (*C. crangon*).

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

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

116

117 **2. Material and methods**

118 *2.1 Collection and maintenance of females*

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

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

131

132 2.2 Larval maintenance

133 The objective was to incubate larvae from 12 clutches (6 winter and 6 summer) at three
134 temperature treatments of 12, 16 and 20°C, as shown in Figure 1. On hatching, actively
135 swimming larvae were separated from females using a pipette. The rostrum-telson length of 30
136 newly hatched larvae from each clutch was measured (Campillo, 1979). For each clutch, 3
137 groups of 104 larvae were distributed in three conical vessels, with filtered seawater at 30 ppt
138 of salinity (± 4), at a density of 100 larvae per L (Reeve, 1969b; Torres et al., 2021). The water
139 was initially at the same temperature as for the maintenance of the females, and then the conical
140 vessels were distributed to 3 incubators (temperature $\pm 0.3^\circ\text{C}$, regulated by a TK700 cooling
141 unit by TECO), with photoperiod 12: 12 (L: D) and constant thin aeration. This resulted in a
142 gradual change which allowed time for the larvae to acclimate to the new temperatures
143 (Richard, 1978). Larvae were fed daily with freshly-hatched *Artemia sp.* nauplii at a density of
144 10 nauplii per mL (Reeve, 1969b). The water was changed (100 %), and larval mortality and
145 development, assessed by identification of stages (see section 2.4), were monitored 3 times a
146 week. During development, the oxygen saturation was 103 % (± 4), the pH was 8 (± 0.1) and
147 the ammonium concentration was 1 mg per L (± 0.3), in mean (\pm S.E.). On moulting to the
148 juvenile stage, shrimps were removed.

149

150 2.3 Intermoult time and number of instars

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

162

163 2.4 Identification of larval stages

164 The different larval stages are identified using morphological criteria. In the larvae of European
165 palaemonidae, the morphological criteria corresponding to the rostrum, caudal region and
166 pleopods are commonly used to identify the different larval stages (Fincham and Figueras,
167 1986). Fincham and Figueras (1986) described 9 larval stages for *P. serratus*, while Campillo
168 (1979) described 6. Description and terminology for the naming of larval stages differ between
169 these authors, but it is possible to do correspondences and characterise 10 different larval stages
170 (Table 1; according to Duflot et al., unpublished). According to these authors, these larval stages
171 are potentially all observable, but are not obligatory stages through which each larvae must pass
172 to develop. On the recent recommendations of Møller *et al.* (2020) regarding the terminology
173 of caridean shrimp larvae, we call these stages zoea 1 to zoea 10 in chronological order of
174 morphogenesis.

175

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	9	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)

179

180

181 2.5 Statistical analysis

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

195

196 3. Results

197 3.1 Zootechnical performances during larval development.

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

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

205 laying season without interaction of these two factors (Deviance analysis, interaction term:
 206 $Chisq = 3.18, p = 0.07$; temperature: $Chisq = 16.19, p < 10^{-5}$; season: $Chisq = 26.6, p < 10^{-7}$;
 207 $n = 6$ per temperature and season).

208 The metamorphoses took place between days 65 and 111 at 12°C, between days 30 and 56 at
 209 16°C and between days 19 and 42 at 20°C (Fig. 2b). The development time of the
 210 metamorphosed larvae varied significantly between the three incubation temperatures, but
 211 neither as a function of the laying season nor as a result of the interaction of these two factors
 212 (Deviance analysis, interaction term: $Chisq = 0.76, p = 0.4$; temperature: $Chisq = 138.73,$
 213 $p < 10^{-16}$; season: $Chisq = 0.62, p = 0.43$; $n = 6$ per temperature and season).

214

215 3.2 Number of instars achieved by larvae.

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

$$219 \quad LIT = 147.96 e^{(-0.25 \text{ temp})} + 2.45 \quad \text{Eq. 1}$$

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

221 This function allows us to calculate the theoretical intermoult times at 12°C (9.8 days), 16°C
 222 (5.2 days) and 20°C (3.4 days) as well as the number of instars achieved by each juvenile
 223 obtained in this experiment. In all experimental conditions, the larvae that metamorphosed did
 224 so after 6 to 13 larval instars (Fig. 4). Only about 3.7 % of them developed for more than 9
 225 instars, and about 1 % for 6 instars. While about 33 and 45 % of the larvae performed 7 instars
 226 at 16 and 20°C, about 43 and 31 % of them performed 8 instars. At 20°C, larvae
 227 metamorphosing after 7 instars represented about 40 % of the total in winter and 50 % in

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

230

231 *3.3 Succession of larval stages.*

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

241 All 10 larval stages described were observed at each temperature. However, we observed
242 differences in the proportions of the different larval stages. At 12, 16 and 20°C, respectively, at
243 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
244 0.3 % of the larvae passed through the zoea 6 stage.

245 Furthermore, during the monitoring of the larval stages presented here, we frequently observed
246 larvae with 2 rostral spines (criteria for zoea 3) and pleopod buds (criteria for zoea 5). This
247 larval stage seems to take place instead of the zoea 3 stage, so we called it zoea 3'. This never
248 described larval stage was not observed at 12°C. At 16 and 20°C, respectively, at least 58.1 and
249 67.8 % of the winter larvae passed through the zoea 3' stage, compared to at least 20.8 and
250 19.9 % of summer larvae.

251

252 4. Discussion

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

257 In contrast to several authors studying the number of larval instars of decapods during
258 development (Reeve, 1969a; Dalley, 1980; Linck, 1995, read in Giménez, 2006), we did not
259 rear the larvae individually. This choice was made in view of the survival rates of *P. serratus*
260 larvae in the laboratory available in the literature. While González-Ortegón and Giménez
261 (2014) and Lassus and Maggi (1980) achieved respectively 40 and 45-70% metamorphosis
262 when rearing larvae individually, Campillo (1979) and Reeve (1969b) achieved respectively 76
263 and over 90% metamorphosis with mass-rearing. Furthermore, Reeve (1969a) observed longer
264 larval development with lower survival when rearing *P. serratus* individually than when mass-
265 rearing.

266 We calculated the number of instars made by the larvae from their average intermoult time
267 according to bibliographic data. Intermoult times obtained for the same temperature may vary
268 slightly between the 6 sources used (Fig. 3). This can be explained by the differences in
269 experimental protocol and by maternal effects. The limited information available on this second
270 factor complicates discussions on this subject. The females used in these 6 experiments came
271 from populations in Ireland, Wales, Brittany and the Mediterranean (the latter being
272 phylogenetically distant from the Atlantic populations; Weiss et al., 2018). Only González-
273 Ortégón and Giménez (2014) specify the period of collection of females (autumn) as well as
274 their size (between 17 and 24 mm from the postorbital margin to the end of carapace, between
275 18 and 22 mm in our study). According to Reeve (1969a) and González-Ortegón and Giménez
276 (2014), the intermoult time of *P. serratus* is constant during larval development under good

277 zootechnical conditions. Nevertheless, these authors reared the larvae of this species between
278 18 and 24°C. It is possible that the intermoult time of *P. serratus* larvae increases as
279 development proceeds at lower temperatures, as reported by Kelly et al. (2012) and Lassus and
280 Maggi (1980) between 10 and 13°C. However, the few individuals that metamorphosed at 12°C
281 leads us to put the interpretation of the number of instars carried out at this temperature into
282 perspective.

283

284 *4.1 Temperature-mediated developmental plasticity*

285 The larval development of *P. serratus* is temperature-driven. Here, metamorphosis rates were
286 temperature dependent (about 2, 36 and 49 % at 12, 16 and 20°C respectively). Campillo (1979)
287 experienced the highest rates of metamorphosis (85 %) by incubating *P. serratus* larvae from
288 Roscoff (France) at 27°C, a temperature above the local maximum. Other authors who studied
289 the larval development of *P. serratus* at temperatures between 10 and 13°C observed a mortality
290 of all individuals between the third and fourth larval instar (Kelly et al., 2012; Lassus and
291 Maggi, 1980; Yagi and Ceccaldi, 1985). We also observed very low survival rates at 12°C, but
292 we managed to get some individuals to metamorphosis (< 2%) after 7-13 instars. We chose to
293 incubate larvae at 12°C because this is the temperature of the sea water in the Bay of Seine
294 (Normandy) at the beginning of May (Claquin et al., 2018), the date at which the larvae from
295 the winter spawning are released by females of the same size as those used for this study
296 (personal observations). Mortality at 12°C was constant during development in the laboratory.
297 At this temperature, only the larvae from 3 of the 12 females suffered mortality rates above
298 50 % by the end of the first instar. The mortality rate of the larvae was approximately 52 %
299 after 30 days of incubation, when most of them were in their fourth instar. The thermal optimum
300 of crustacean larvae experiences an ontogenic shift (Sastry and McCarthy, 1973). These
301 variations between larval stages are due to temperature-induced changes in metabolic rates

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

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

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

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

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

338 These differences in survival between thermal conditions can also be explained by differences
339 in nutritional requirements. Crustacean larvae require long-chain polyunsaturated fatty acids
340 (PUFAs) for development, such as eicosapentaenoic acid, or EPA, and docosahexaenoic acid,
341 or DHA (Anger, 1998; Bergé and Barnathan, 2005). These are generally synthesised by
342 phytoplankton and transferred into the food chain (Lubzens et al., 1995). PUFAs, DHA in
343 particular, maintain membrane integrity and viscosity (Estévez and Kanazawa, 1996; Los and
344 Murata, 2004; Pagliarani et al., 1986), especially in cold waters (Harwood, 1988; Munro and
345 Thomas, 2004). Like many authors, we fed *P. serratus* larvae with artemia nauplii (Campillo,
346 1979; Reeve, 1969b; Wickins, 1972; Yúfera and Rodríguez, 1985). Although these are
347 traditionally used to feed decapod larvae, they are known to be deficient in PUFAs (Narciso
348 and Morais, 2001; Navarro et al., 1999). These deficiencies may explain the very low survival
349 of *P. serratus* larvae in cold water observed here and by the authors mentioned in the paragraph
350 above. PUFAs also influence growth, stress and disease resistance in decapods (Anger, 1998;
351 Kanazawa et al., 1985; Mourente and Rodríguez, 1997). It would be interesting to study the

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

354

355 4.2 Developmental plasticity induced by laying season and its interaction with temperature

356 The newly hatched larvae used in this study were larger in winter than in summer. These results
357 are consistent with González-Ortegón *et al.* (2018) who observed difference in *P. serratus*
358 larval biomass between laying seasons. Because of this difference in phenotype, we
359 hypothesised that *P. serratus* larvae from winter females would develop faster than those from
360 summer females. These effects were not significant in our data analyses. At a given
361 temperature, summer larvae even appeared to perform fewer larval instars than winter larvae.
362 These results are in contradiction with those obtained on another caridean shrimp species
363 (Linck, 1995, read in Giménez, 2006). The author incubated larvae of *C. crangon*, from large
364 winter eggs and small summer eggs, at two relatively cold and warm temperatures (12 and
365 18°C). Regardless of the temperature, summer larvae metamorphosed after a greater number of
366 larval instars than winter larvae. We need to further investigate the effects of the interaction
367 between the laying season and environmental conditions on the developmental plasticity of
368 *P. serratus*.

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

376 larval biomass in *P. serratus* larvae under starvation conditions, González-Ortegón & Giménez
377 (2014) did not confirm this trend under favourable feeding conditions. This result is consistent
378 with those presented here.

379 Although the development time of the larvae in the two laying seasons did not differ, at 16 and
380 20°C, the zoea 3' stage was observed more often in winter larvae than in summer larvae (Fig. 5
381 to 7). The morphogenesis of the winter larvae (pleopod buds) was earlier than that of the
382 summer larvae, at least in the early larval stages. The winter larvae may have received more
383 available energy resources (transmitted by the mother) than summer larvae and used them
384 during these early instars. This phenomenon may have been favoured by the choice of females
385 used. The cephalothorax of the winter females measured on average about 40 mm. These would
386 be more than two years old, which corresponds to less than 2 % of the female population of
387 *P. serratus* (Campillo, 1979). The limited information available on the size of the females and
388 the date of their sampling in previous publications does not allow comparison of our results.
389 The lack of description of the zoea 3' stage in previous studies can be explained by the choice
390 of females used. We need to investigate the effects of female age on maternal investment and
391 developmental plasticity in *P. serratus*.

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

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

404 In *P. serratus*, winter larvae are larger than summer larvae. We expected that this phenotypic
405 difference would allow winter larvae to develop faster than summer larvae at the same
406 temperature. Although we did not observe this result, we did observe earlier morphogenesis in
407 winter larvae at the warmest temperatures. As explained in the previous paragraphs (see section
408 4.2), we believe that this phenomenon is related to the amount of energy allocated per offspring.
409 This pattern of maternal investment buffers winter larvae from variable early season conditions
410 (low temperature, Torres et al., 2020; less abundant planktonic food resources, Paschke et al.,
411 2004). Furthermore, the negative effects of food limitation on larval survival are exacerbated
412 by unfavourable temperatures (Torres and Giménez, 2020). The few months separating the
413 hatching of the larvae from the two laying periods of *P. serratus* result in two cohorts of
414 juveniles (Campillo, 1979). As these cohorts share the same habitats, they compete for
415 resources or even cannibalise (Moksnes et al., 1998). The shift in the recruitment periods of
416 these two cohorts results in a difference in the size of the individuals (*P. serratus* juveniles of
417 0.5g which double or triple their weight in 2 months depending on their sex at temperatures
418 between 18 and 29°C; Rodriguez, 1981). These traits probably favour juveniles from winter
419 laying over those from summer laying in years when early season conditions are favourable
420 (Temming et al., 2017). The population structure and dynamics of *P. serratus* should be studied
421 to assess the settlement success of winter and summer cohort. This would facilitate
422 understanding the effects of juvenile recruitment phenology on their interactions.

423

424 *Conclusion*

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

430

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436

437 **Vitae**

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

441

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

446

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

449

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

452

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

456

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

464

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

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

471

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- 705

706 **Figure captions**

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

712

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

718

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

723

724 Figure 4: The relative frequency (%) of the total number of larval instars reached by
725 metamorphosed *Palaemon serratus* larvae. Larvae are grouped by laying season and incubation
726 temperature; W12: Winter 12°C (n = 18), S12: Summer 12°C (n = 5), W16: Winter 16°C (n =
727 186), S16: Summer 16°C (n = 257), W20: Winter 20°C (n = 271) and S20: Summer 20°C (n =
728 350).

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

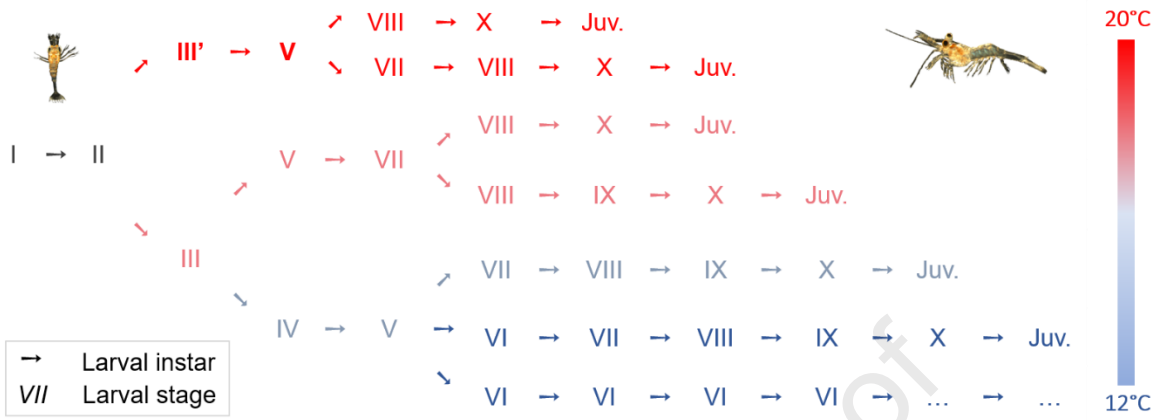
742 Figure 7: Number of *Palaemon serratus* larvae observed for each larval stage during their
743 development at 20°C. Larvae are grouped by clutch; 1 to 6: winter females, 7 to 12: summer
744 females (n = 104 larvae per female). Juveniles are removed at metamorphosis and their
745 cumulative numbers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

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Graphical abstract

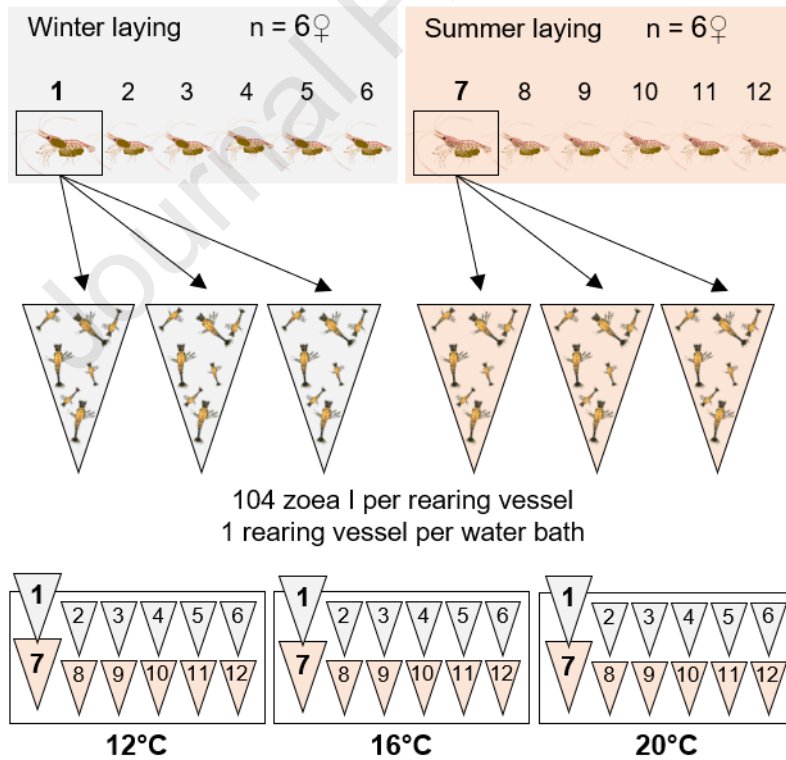
Most frequent developmental pathways in relation to temperature with winter and summer larvae



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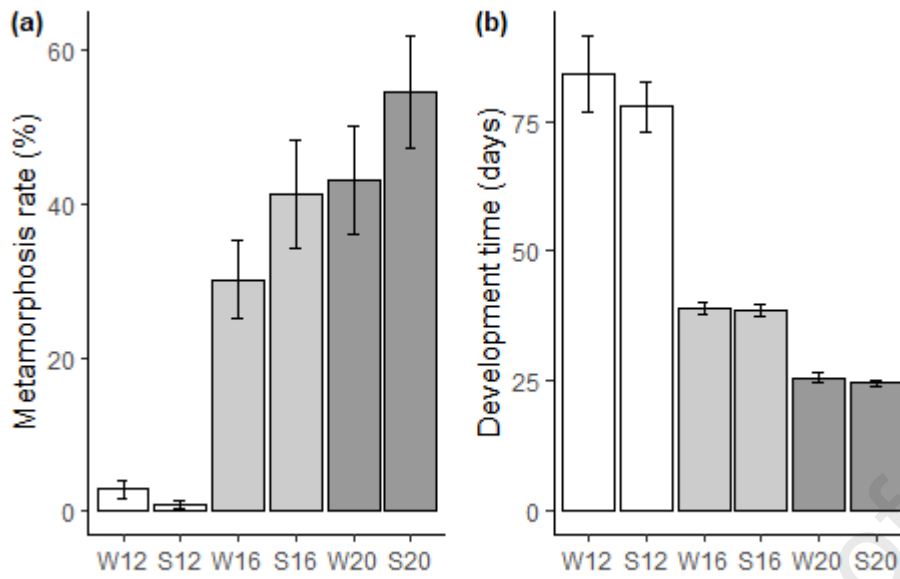
751 Figures



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753 Figure 1

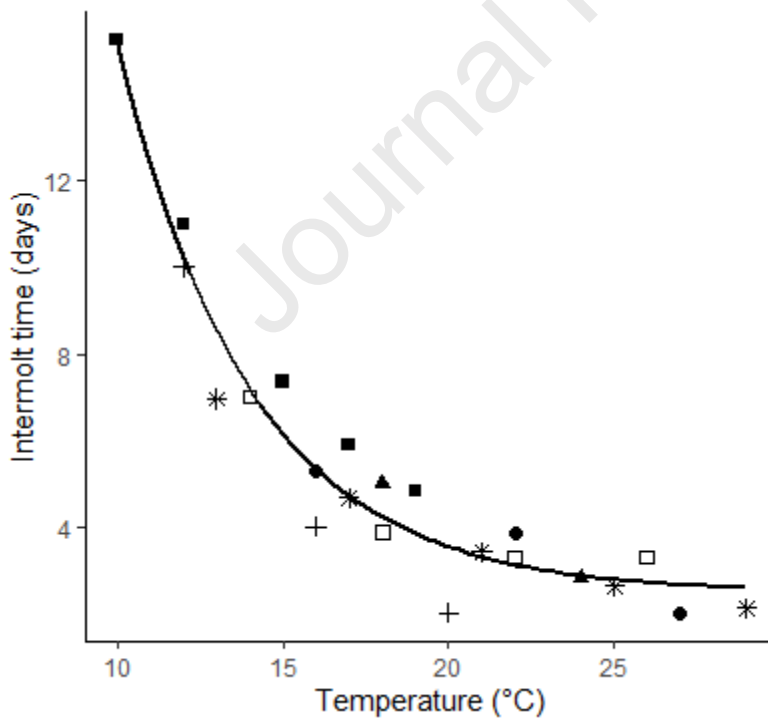
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756 Figure 2

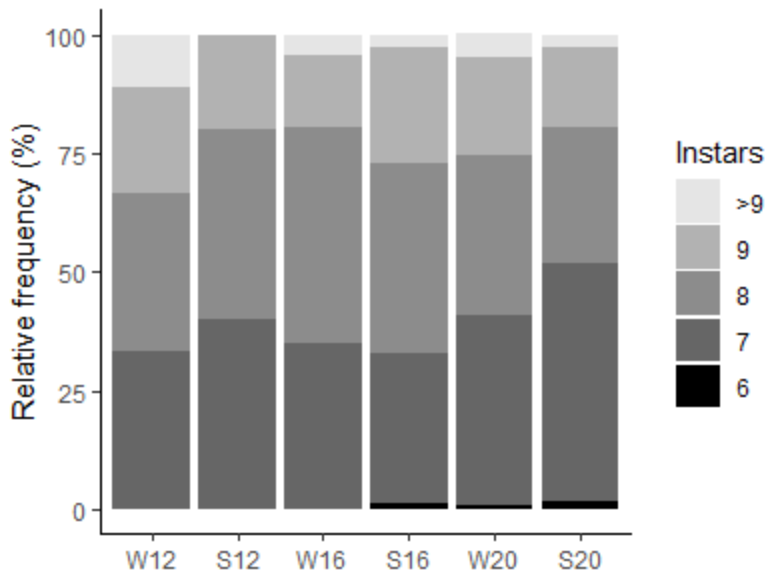
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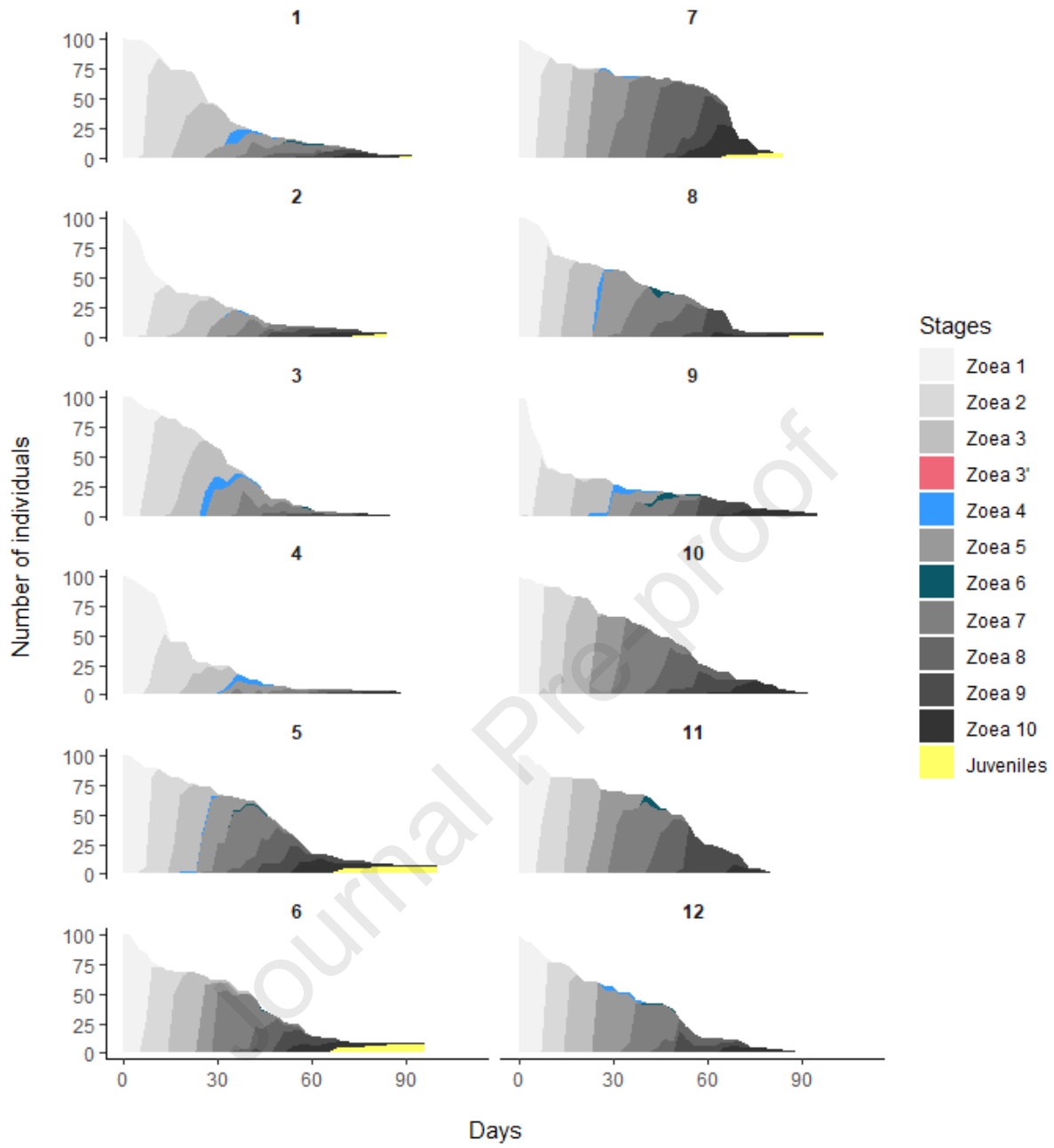
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762 Figure 4

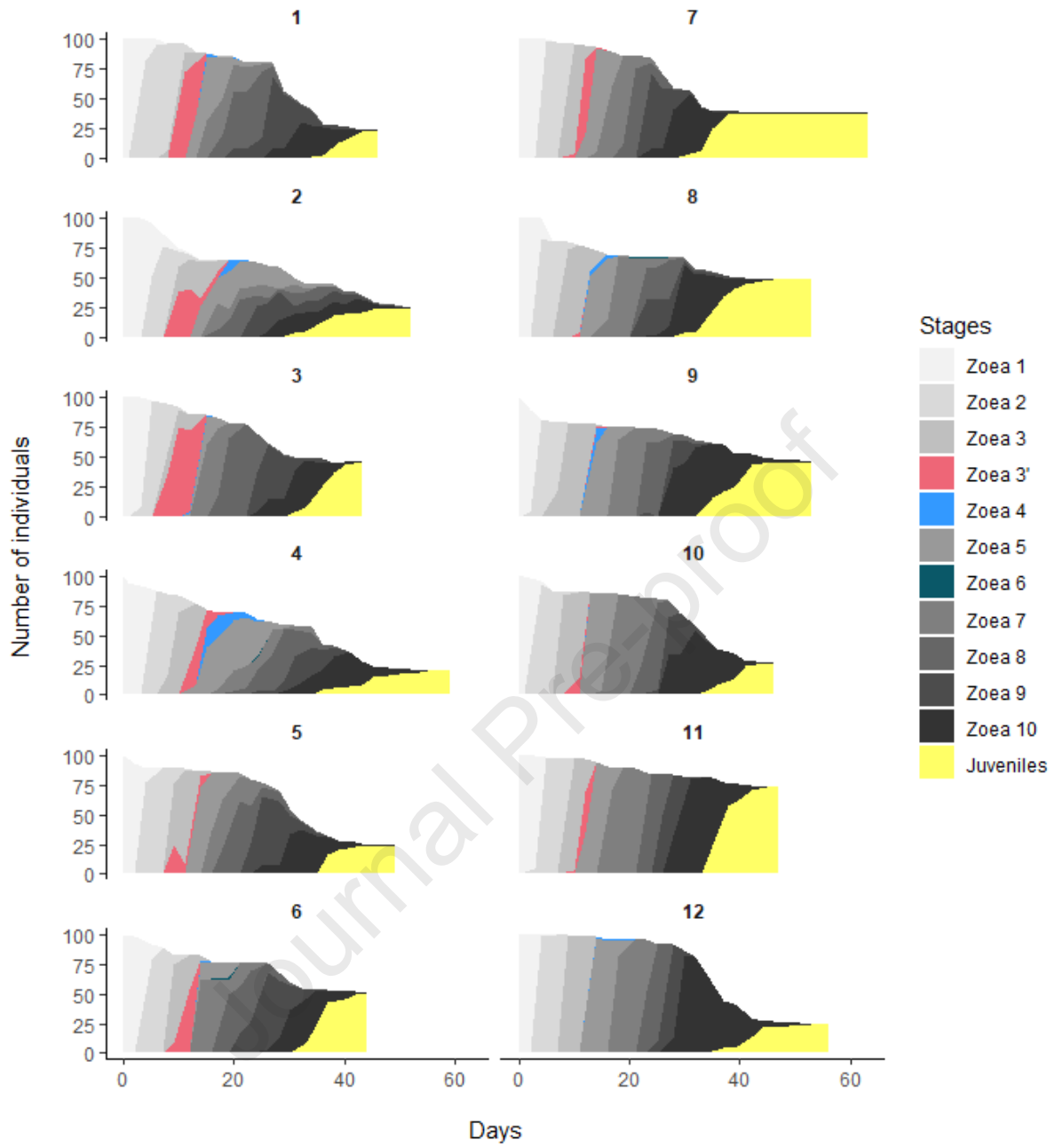
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765 Figure 5

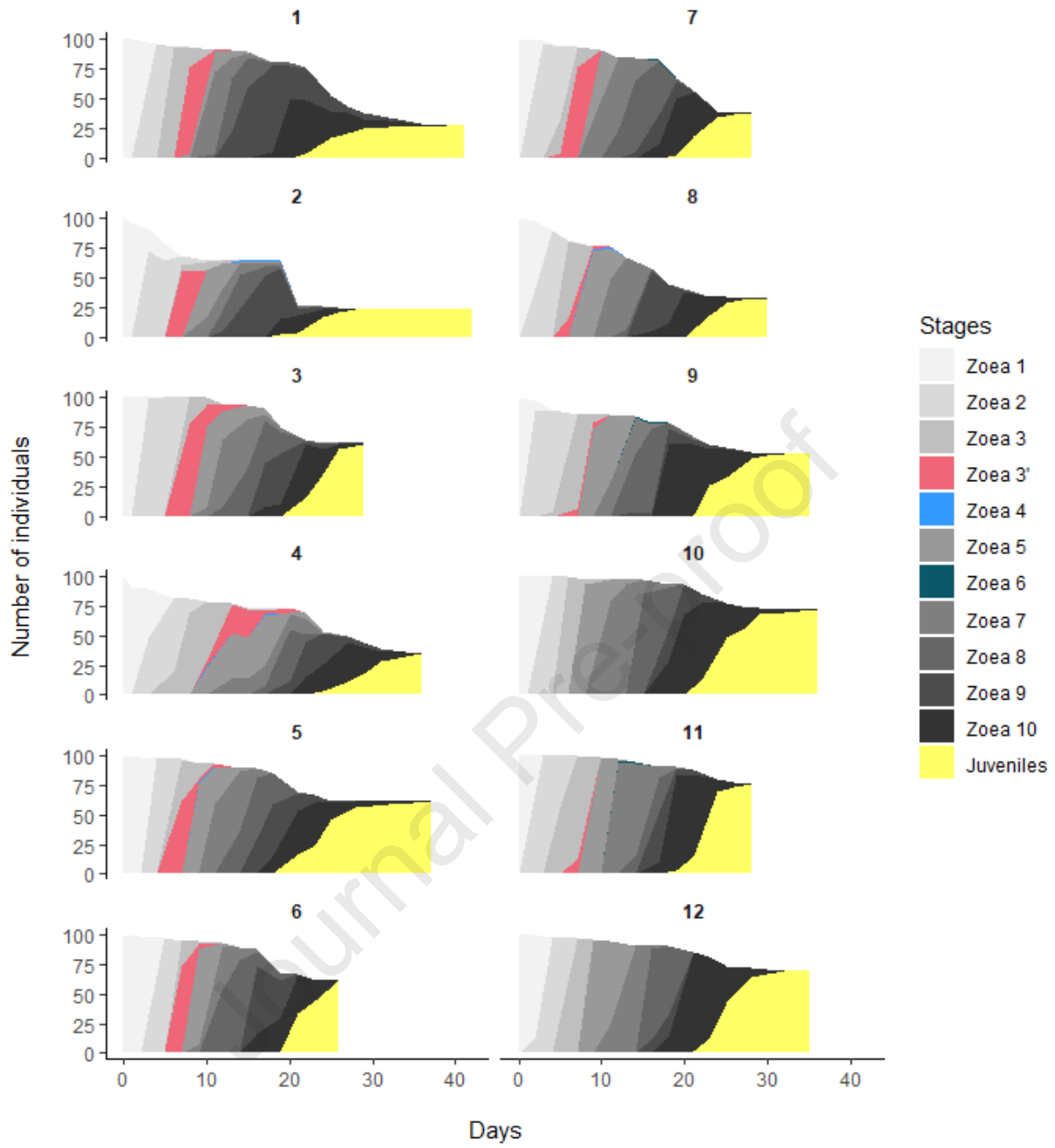
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768 Figure 6

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771 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.

Journal Pre-proof

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Journal Pre-proof