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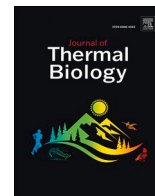
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Combined effects of temperature and diet on the performance of larvae produced by young and old *Palaemon serratus* females

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ABSTRACT

Seasonal variations in environmental conditions determine the success of decapod larval development, and females transmit more energy in sub-optimal conditions to maximise the *fitness* of their offspring. The objective of this study was to focus on the combined effects of temperature (14, 18 and 22 °C) and food quality on the performance of larvae produced by 5 young (0+) and 5 old (I+) *Palaemon serratus* females. We prepared 3 diets based on Artemia, in decreasing order of total fatty acid content: freshly hatched nauplii (N), unenriched metanauplii (M) and metanauplii enriched with a mixture of microalgae (ME). At hatching, the larvae produced by I+ females had a higher biomass but a similar fatty acid concentration to those produced by 0+ females. Larvae survived better and developed relatively faster as temperature increased, and the longer they waited to metamorphose, the greater their weight at metamorphosis. These performances were diet-dependent, with more survival and more growth in less time with diet N than with the other two. Larvae from I+ females performed better than those from 0+ females, especially under the most stressful conditions. The greater biomass of the larvae of I+ females seems to have enabled them to follow a shorter, and therefore faster, development path than those of 0+ females. The larvae's diet also had an impact on post-metamorphic composition: larvae eating a diet richer in fatty acids produced richer juveniles and those eating a poorer diet produced juveniles with slightly more essential fatty acids. This study supports the high plasticity of caridean shrimp larval development and the importance of maternal effects on the fitness of offspring.

1. Introduction

Seasonal variation in planktonic conditions determines the developmental success of decapod larvae. Temperature is a well-known environmental parameter influencing the larval development of crustaceans. It determines the feeding activity of the organisms, their metabolism and therefore their survival (Ravi and Manisseri, 2012; Leiva et al., 2022; Tills et al., 2022). The duration of larval development is strongly temperature dependent as increasing temperature allows a decrease in the number of larval instars and their duration (Knowlton, 1974; Ostrensky et al., 1997; O'Connor et al., 2007) as well as a modification of the larval stages carried out until the metamorphosis (Crfales and Anger, 1986; Oliphant et al., 2013; Baudet et al., 2022). Food also plays a key role during larval development. Food availability determines

the success and duration of larval development (Anger and Dawirs, 1982; Anger, 1987b), but also the growth of juveniles after metamorphosis (Giménez, 2010). Several authors have studied the effects of the duration of food availability on larval performance (Giménez and Anger, 2005; D'Urban Jackson et al., 2014; Torres and Giménez, 2020). These studies were based on the observation that since decapod larvae surface in food patches for only a few hours per day during diel vertical migration, the duration of food availability is generally limited (Abello and Guerao, 1999; dos Santos et al., 2008). In contrast, very few authors have studied the effects of food quality on the larval development success (Calado et al., 2008, 2022).

Marine decapod larvae are planktonic and display a wide range of feeding strategies (Jones et al., 1997). Carnivorous larvae feed mainly on micro and mesozooplankton such as copepods in the nauplii or adult

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stages depending on the species (Stickney and Perkins, 1981; Harding et al., 1983). Herbivorous copepods accumulate lipids from phytoplankton (especially fatty acids) and biosynthesize fatty acids that are absent from their diet (Graeve et al., 2005; Yamada et al., 2016). In the North Atlantic, zooplankton is mainly composed of calanoid copepods which are very lipid-rich (Gatten et al., 1979; Kattner and Krause, 1989; Jónasdóttir, 1999; Lenz et al., 2012). These copepods can respond to seasonal conditions (temperature and food supply) by accumulating more lipids and fatty acid during spring and summer phytoplankton blooms, and then relying on their reserves during winter (Kattner and Krause, 1989). This variability in copepod lipid content plays a fundamental role in global marine food webs (Jónasdóttir et al., 2015; Record et al., 2018).

Decapod larvae need mainly proteins, lipids and carbohydrates for growth and development (Anger, 2001; Jeffs and O'Rorke, 2020). Among lipids, phospholipids are key structures of membrane cells while triacylglycerides (TAG) represent the main form of storage in the hepatopancreas of decapod larvae (Briggs et al., 1988; Chang and O'Connor, 2012). Fatty acids fulfil these two roles depending on their length and unsaturation level (Parzanini et al., 2023). Long-chain polyunsaturated fatty acids are crucial for the development of decapod larvae and, when limited, have effects on stress, developmental stages and ultimately survival (Kanazawa et al., 1985; Mourente and Rodríguez, 1997). Thus, the content of long-chain fatty acids in larval tissues is considered an indicator of good fitness (Kanazawa et al., 1985; Ouellet et al., 1992; Kattner et al., 1994a; Mourente and Rodríguez, 1997; Takeuchi et al., 1999a; b; D'Souza and Kelly, 2000). Among long-chain fatty acids, eicosapentaenoic (EPA; 20:5n-3), docosahexaenoic (DHA, 22:6n-3) and arachidonic (ARA; 20:4n-6) acids are called essential and are preferentially retained in the tissues of aquatic organisms (Kainz et al., 2004; Mezek et al., 2010). Decapod larvae assimilate fatty acids from their diet and have a low capacity to biosynthesize essential fatty acids (Kanazawa et al., 1979b, 1979a; Jones et al., 1979; Roustaiian et al., 1999). To maximise their fitness, female decapods are able to produce larger and richer offspring as they age (Attard and Hudon, 1987; Clarke, 1993; Tully et al., 2001; Giménez and Anger, 2001; Smith and Ritar, 2007; Fischer et al., 2009; Emmerson et al., 2017).

The energy transmitted to offspring by the mother affects larval performance in decapods. Marine decapods are often planktotrophic (need to feed during larval development), although many are capable of facultative lecithotrophy during the early larval stages (no need to feed). This ability is enabled by the yolk reserves available at hatching (Kattner et al., 2003; Oliphant and Thatje, 2014; Brown et al., 2019). On an intra-specific scale, larvae with a higher hatching biomass and long-chain fatty acids content have a better chance of survival and develop more rapidly (Cavalli et al., 1999; Paschke et al., 2004; Brown et al., 2019). This is especially true under conditions of thermal, saline or starvation stress (González-Ortegón and Giménez, 2014).

The European shrimp *Palaemon serratus* has a larval development known to be temperature mediated between 14 and 27 °C (Fincham and Figueras, 1986; Kelly et al., 2012; González-Ortegón and Giménez, 2014). It requires between 6 and 9 planktonic zoeal stages, that are able to feed as soon as they hatch, before they metamorphose into juveniles (Campillo, 1979; Fincham and Figueras, 1986). Females live from 2 to 5 years and reproduce twice a year, once in winter resulting in a spring hatch and once in spring resulting in a summer hatch (Campillo, 1979). Larval biomass and lipid content at hatching is higher in winter broods and older females, although it is difficult to disentangle the effect of age and season (González-Ortegón et al., 2018; Baudet et al., 2022, 2023b). Experimentally, *P. serratus* larvae are generally fed with *Artemia* nauplii (Reeve, 1969; Campillo, 1979). This food is known to be rich in total lipids, but low in long-chain fatty acids like DHA (Navarro et al., 1999; Narciso and Morais, 2001). As they develop, *Artemia* nauplii become depleted in lipids (Evjemo et al., 2001). Therefore, in aquaculture, *Artemia* are enriched with long-chain lipids using microalgae

(Sargent et al., 1999; Evjemo et al., 2001; Copeman et al., 2002). Distribution of *Artemia* nauplii enriched with *Isochrysis galbana* increased the rate of metamorphosis in *P. serratus* (Wickins, 1972).

The present study aimed to better understand how fitness could be maximized during larval development in a decapod species living in a seasonal environment, with metamorphosis rate, development time, larval growth and fatty acid composition of juveniles to assess fitness during development. Larvae produced by young and old females were incubated at 3 temperatures and fed 3 different diets. The fatty acid content and composition of the distributed diets and of the larvae at hatching were measured as prerequisites. This allowed the following three questions to be answered: 1) What is the plastic response of larvae to dietary stress (particularly low fatty acid content)? 2) Does a good quality diet (i.e. rich in long-chain fatty acid) compensate for the negative effects of temperature? 3) How do females maximise the fitness of their offspring as they age?

2. Materials and methods

2.1. Collection and maintenance of egg-bearing females

Ten females of *P. serratus* carrying eggs at the end of their development (stage E-H; Richard, 1974) were sampled with hand nets on the foreshore of the Chausey archipelago (48.876091N, -1.834105W, Manche, France; Decision No. 286/2020, Interregional Directorate of the Sea Eastern Channel-North Sea). Five class I+ were caught on 18/05/2022 and measured 37.6 ± 0.8 mm (the average of cephalothorax length \pm S.E.). Five class 0+ were caught on 13/07/2022 and measured 29 ± 0.6 mm (average \pm S.E.). The age classes were determined following those given by Campillo (1979) according to their cephalothorax length. The shrimp were transferred to the laboratory of the University of Le Havre, then maintained under a 12:12 (L:D) photoperiod in a 100 L temperature-controlled tank at 18 °C, filled with natural filtered and aerated seawater at 32.2 ± 1.7 (average \pm S.D.) of salinity (Fig. 1). The seawater was renewed by half 3 times a week to avoid ammonium build-up. Each specimen was isolated in wire baskets covered with fine mesh and fed individually twice a week *ad libitum* with squid pieces. Larvae were checked daily for hatching.

2.2. Larval maintenance

Groups of larvae from the 10 females were incubated at 3 temperature treatments (14, 18 and 22 °C) and on 3 different diets, each group from a single female (Fig. 1). At hatching, actively swimming larvae were separated from females using a pipette. For each brood, 9 groups of 50 larvae were released into 9 conical vessels, with filtered seawater (salinity = 30 ± 1.6 PSU), at a density of 100 larvae per L as recommended (Reeve, 1969). The water was initially at 18 °C (i.e. the same temperature as for female maintenance) and then the conical vessels were distributed by 3 in 3 incubators (temperature ± 0.1 °C, regulated by a TECO TK700 cooling unit and continuously measured with a temperature logger), with a 12 : 12 (L : D) photoperiod and constant gentle aeration. This allowed a gradual change of about 15 min for the larvae to acclimatise to the new temperatures (Richard, 1978). Three times a week, the water was changed at 100 %, larval mortality and developmental stage were monitored. Simultaneously to water change, physico-chemical parameters were measured once a week (Table 1). Temperature was measured every minute in a container throughout larval development, using an immersed probe.

At the 3rd larval instar, each larva was observed to determine whether it had the morphological criteria of the zoea 3 or zoea 3' stage. In contrast to the zoea 3 stage, the zoea 3' stage has pleopod buds which indicate an abbreviated larval development (Baudet et al., 2022). Upon metamorphosis into juvenile (rostrum with more than 6 teeth and benthic behaviour, Fincham and Figueras, 1986), the shrimp were removed.

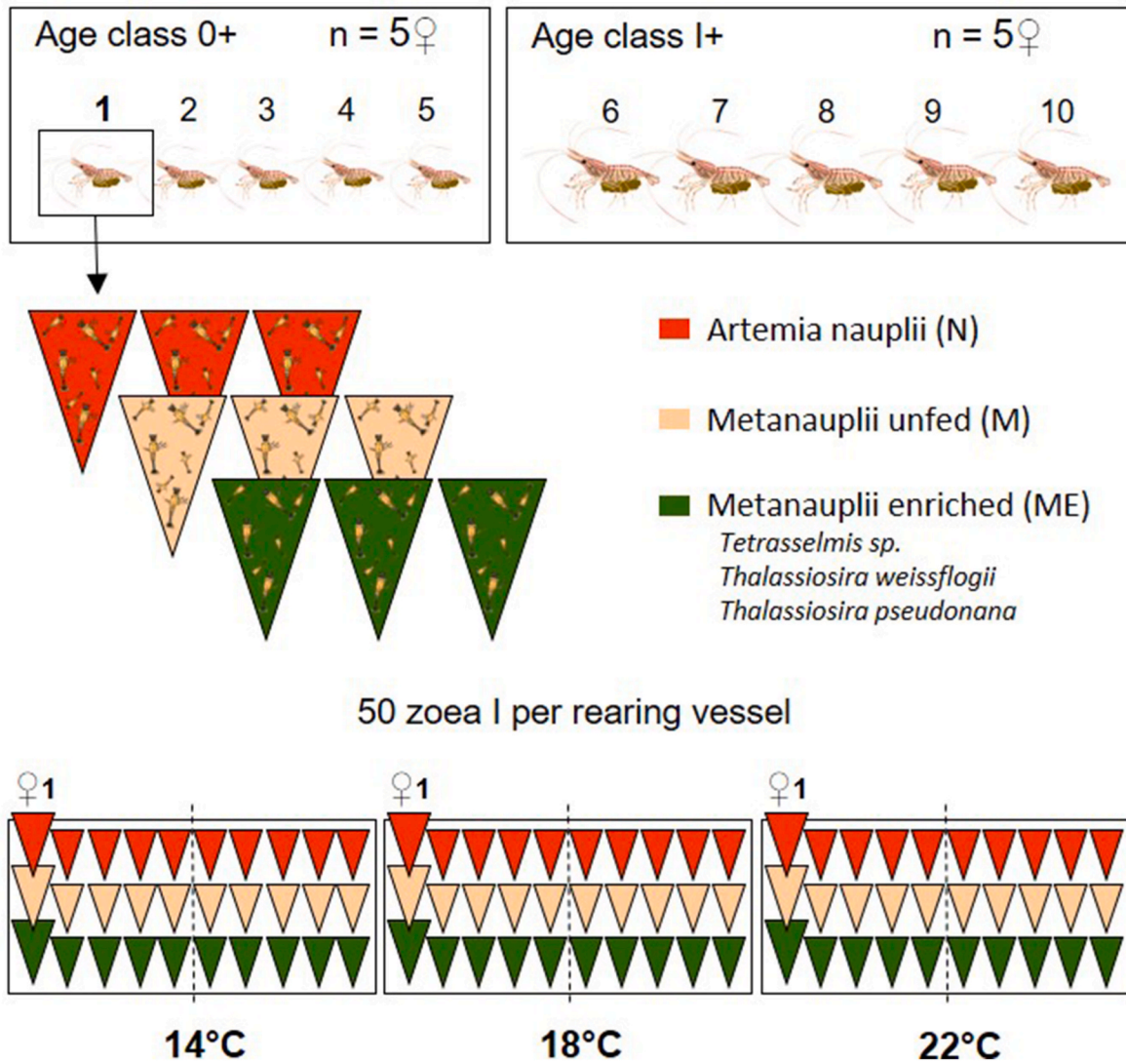


Fig. 1. Experimental design to study the effects of temperature, diet and maternal age on plasticity of larval development in *Palaemon serratus*. For the 10 females (5 class 0+ and 5 class I+), the larvae are distributed in conical containers in 3 water baths following the illustrated example of the larvae of female 1. The illustrations of the females are modified from the one available on the Muséum-Aquarium de Nancy website by Marion Arbona.

Table 1
Average physico-chemical conditions (\pm S.D.) in the 3 thermal conditions during maintenance of *Palaemon serratus* larvae.

| Water-bath | 14 °C | 18 °C | 22 °C |
|--------------------------------|-------------------|-------------------|-------------------|
| Temperature (°C) | 14.07 \pm 0.01 | 18.04 \pm 0.01 | 22.07 \pm 0.01 |
| Dissolved oxygen (%) | 107.17 \pm 4.03 | 104.85 \pm 2.61 | 103.92 \pm 2.20 |
| Salinity | 32.37 \pm 1.62 | 32.16 \pm 1.66 | 32.06 \pm 1.72 |
| pH | 8.15 \pm 0,02 | 8.13 \pm 0,04 | 8.06 \pm 0.04 |
| Ammonium (mg L ⁻¹) | 0.86 \pm 0,33 | 1 \pm 0.45 | 1.11 \pm 0.44 |

2.3. Diets

Three diets of *Artemia salina* were prepared daily. Cysts (INVE SEPART Artemia Cysts) were hydrated and then incubated with aerated seawater at a salinity of 25 PSU in a 0.5L conical system incubated in a water bath at 30 °C and illuminated at 12:12 photoperiod. The diet “N” consisted of freshly hatched *Artemia* nauplii I and II (about 0.52 mm long) harvested 24 h after incubation at a density of 250 000 nauplii/L., filtered and restocked with new water. For the next two diets, nauplii reared and harvested under the same conditions were restocked for a further 24 h in new water at a density of 125 000 nauplii/L. The diet “M”

consisted of unfed metanauplii I of *Artemia* 24 h after hatching (about 0.71 mm long). The diet “ME” was metanauplii I of *Artemia* 24 h after hatching (about 0.77 mm long) and enriched with a mixture of 3 microalgae in excess (*Tetrasselmis* sp., *Thalassiosira weissflogii* and *T. pseudonana*, PLANKTOVIE LPB Frozen Shellfish Diet). For each brood and water bath, one of the 3 conical vessels was fed daily with one of the 3 diets (Fig. 1), at a density of 10 *Artemia* per mL (Reeve, 1969). A sample of over 2g fresh weight of each of the 3 *Artemia* diets and the algal diet was frozen at -80 °C for fatty acid analysis.

2.4. Biometrics of offspring

At hatching of each brood, 3 pools of 100 larvae were weighed to obtain the average weight of each brood. A pool of 100 larvae from each brood was then frozen at -80 °C for fatty acid analysis. At metamorphosis, the juveniles were weighed individually. For each conical vessel (i.e. each brood in one condition), 2 pools of juveniles (i.e. 3-5 individuals) were frozen at -80 °C for fatty acid analysis (i.e. 131 pools in total). The first pool was composed of juveniles that metamorphosed after 7 instars while the second pool had reached metamorphosis after 9 instars. We estimated the number of instars performed by dividing the development time of each individual by the theoretical

average intermolt time, as explained in Baudet et al. (2022).

2.5. Fatty acid content analysis

The total fatty acid content and composition of samples frozen at -80°C (diets, pools of hatched larvae, pools of juveniles) were measured. The diet samples were freeze-dried for 24 h, but the larval and juvenile pools were not. After grinding, lipids samples were extracted with a mixture of chloroform and methanol (2:1, v:v) and immersion in an ultrasound bath. Analytical procedure followed (Mathieu-Resuge et al., 2019), where 1 mL of extract was first saponified by adding 1 mL of KOH–MeOH and heating at 80°C for 30 min, before being transmethylated by adding 1.6 mL of a MeOH–H₂SO₄ mixture (3.4 %; v:v) and heating at 100°C for 10 min. C23:0 was used as an internal standard for fatty acid quantification. Gas chromatography analysis was carried out on a Varian CP8400 gas chromatograph using two separations simultaneously on a polar column (Front, ZBWAX: 30 mm \times 0.25 mm ID \times 0.25 μm , Phenomenex) and a non-polar column (Middle, ZB5HT: 30 m \times 0.25 mm ID \times 0.25 μm , Phenomenex). The temperature program used by the GC consisted of an initial heating from 60°C to 150°C at $50^{\circ}\text{C}\cdot\text{min}^{-1}$, then to 170°C at $3.5^{\circ}\text{C}\cdot\text{min}^{-1}$, to 185°C at $1.5^{\circ}\text{C}\cdot\text{min}^{-1}$, to 225°C at $2.4^{\circ}\text{C}\cdot\text{min}^{-1}$, and finally to 250°C at $5.5^{\circ}\text{C}\cdot\text{min}^{-1}$ and maintained for 25 min.

2.6. Statistical analysis

Statistical procedures were implemented with R 4.3.1 software (R Core Team, 2023). The difference in larval weight between the broods of 0+ and I+ females was tested using a Student's t-test. To test the effects of temperature, diet, maternal age and duration of development on larval performance, we used mixed-effects models to consider that for a given maternal age (i.e. 0+ or I+) the larvae used at different conditions (temperature and diet) were from the same females. For the rate of metamorphosis of each brood and the proportion of larvae developing through the zoea 3' stage, we fitted a generalised linear mixed effects model with a logit link function and a binomial error distribution (*glmer* function from the *lme4* package; Bates et al., 2015) and performed a deviance analysis procedure including interaction terms (using the *car* package). For duration of development and weight, we fitted a linear mixed effects model (using the *lmer* function of the *lme4* package; Bates et al., 2015). *P* values were estimated using *lmerTest* package (Kuznetsova et al., 2017). To test the effects of temperature, diet, maternal age and duration of development on fatty acid composition, we used Permutational Multivariate Analysis of Variance tests (PERMANOVA; Anderson, 2001) using the *adonis2* function with Bray–Curtis distance of the *vegan* package (Oksanen et al., 2022). The fatty acid compositions of the different conditions were also compared using PCA analyses performed with the *FactoMineR* package (Lê et al., 2008). PERMANOVA and PCA analysis included only fatty acids representing at least 1 % of the total fatty acid composition in at least one of the samples.

3. Results

3.1. Diet composition

The total fatty acid concentration of the N, M and ME *Artemia* diets were 120.90, 99.44 and 87.28 $\mu\text{g}/\text{mg}$ dry weight respectively. Their fatty acid relative composition were similar (Table 2; Fig. 2A). The concentration of the algal diet used to enrich the ME diet was 47.97 $\mu\text{g}/\text{mg}$ dry weight. It contained relatively more polyunsaturated fatty acids and long-chain fatty acids than the *Artemia* diets (Table 2; Fig. 2A). The most concentrated fatty acids were 16:0, 18:1n-7, 18:1n-9 and 18:3n-3 in all *Artemia* diets and 16:0, 16:1n-7, 16:4n-3 and 22:6n-3 (DHA) in algal diet (Table 2). DHA represented 6.8 % of fatty acids in the algal diet and was absent from all three *Artemia* diets. EPA (20:5n-3) represented 2.2, 3.0 and 3.2 % while ARA (20:4n-6) represented 0.6, 0.9 and 1.0 % of

Table 2

Relative FA composition (%) of the 3 *Artemia* diets (N: hatched nauplii, M: unfed metanauplii, ME: metanauplii enriched with microalgae) and the algae. Results are summarised by FA category and FAs accounting for more than 1 % of the total in at least 1 sample are presented.

| | N | M | ME | Algae |
|-----------------|--------|--------|--------|--------|
| 14:0 | 0.6 % | 0.6 % | 0.6 % | 4.7 % |
| 16:0 | 10.5 % | 10.2 % | 10.3 % | 18.0 % |
| 18:0 | 4.3 % | 5.9 % | 6.2 % | 0.6 % |
| 16:1n-7 | 2.5 % | 2.2 % | 2.2 % | 6.8 % |
| 16:1n-9 | 0.7 % | 0.7 % | 0.7 % | 2.8 % |
| 18:1n-7 | 5.8 % | 7.8 % | 8.2 % | 1.4 % |
| 18:1n-9 | 20.1 % | 20.0 % | 19.7 % | 4.2 % |
| 16:2n-4 | 0.1 % | 0.1 % | 0.1 % | 3.8 % |
| 16:3n-3 | 1.3 % | 1.1 % | 1.1 % | 0.4 % |
| 16:3n-4 | 0.0 % | 0.0 % | 0.0 % | 5.6 % |
| 16:4n-3 | 0.3 % | 0.2 % | 0.2 % | 7.8 % |
| 18:2n-6 | 6.5 % | 5.9 % | 5.8 % | 3.3 % |
| 18:3n-3 | 29.7 % | 26.6 % | 26.0 % | 5.0 % |
| 18:3n-6 | 0.4 % | 0.3 % | 0.3 % | 1.3 % |
| 18:4n-3 | 4.8 % | 4.1 % | 4.0 % | 1.6 % |
| 18:5n-3 | 0.0 % | 0.0 % | 0.0 % | 3.3 % |
| ARA | 0.6 % | 0.9 % | 1.0 % | 0.9 % |
| EPA | 2.2 % | 3.0 % | 3.2 % | 4.3 % |
| 22:5n-6 | 0.0 % | 0.0 % | 0.0 % | 2.2 % |
| DHA | 0.0 % | 0.0 % | 0.0 % | 6.8 % |
| Totals | | | | |
| Branched | 3.6 % | 3.8 % | 3.7 % | 0.3 % |
| SFA | 16.6 % | 18.1 % | 18.6 % | 25.2 % |
| MUFA | 30.3 % | 32.0 % | 32.2 % | 18.6 % |
| PUFA | 49.3 % | 45.8 % | 45.4 % | 51.2 % |
| NMI | 0.0 % | 0.0 % | 0.0 % | 0.0 % |
| DMA | 0.0 % | 0.0 % | 0.0 % | 0.0 % |
| Unknown | 0.3 % | 0.4 % | 0.1 % | 4.4 % |

the N, M and ME diets respectively and 4.3 and 0.9 % of the algal diet respectively.

3.2. Hatching weight and larval fatty acid composition

The hatching biomass of the larvae from class 0+ females was smaller than that of the larvae from class I+ females (in average 0.28 ± 0.01 and 0.34 ± 0.01 mg respectively, \pm S.E.; t-test *p*-value $< 10^{-3}$). At hatching, the larvae of class 0+ and I+ females contained on average 3.73 ± 0.31 and 4.69 ± 0.52 μg wet weight fatty acid (\pm S.E.) respectively. There was no difference in the proportion of each type of fatty acid between the larvae produced by both age class of females (Fig. 2B, Table 3). Polyunsaturated fatty acids represented 43.9 and 42.2 % of the total fatty acids contained in the larvae of 0+ and I+ females respectively. The most concentrated fatty acids were 18:0, 18:1n-9, EPA and DHA in all broods (Table 3). EPA and DHA represented 18 and 18.8 % and 11.6 and 10.7 % of the fatty acids of young and old female larvae, respectively.

3.3. Larval development of broods

Of the 4500 larvae incubated in this study, we obtained 2206 juveniles. The interaction between temperature, diet and maternal age affected the rate of larval metamorphosis (Table 4 and S1; Fig. 3A). The rate of metamorphosis increased with temperature (39.43 ± 5.15 , 45.43 ± 4.78 and 65.80 ± 0.85 % respectively at 14, 18 and 22°C , \pm S.E.; Table 4; Fig. 3A). At 14°C on all three diets and at 22°C on diets M and ME, the rate of metamorphosis of larvae from young females was lower than that of larvae from old females (respectively 29.53 ± 0.61 and 49.33 ± 0.51 at 14°C and 50.20 ± 1.94 and 75.00 ± 2.1 % at 22°C , \pm S.E.). At 22°C for larvae from young females, the rate of metamorphosis was lower with the M and ME diets than with the N diet (49.60 ± 13.29 , 50.28 ± 9.48 and 74 ± 2.97 % respectively, \pm S.E.).

The interaction between temperature and diet, the interaction between temperature and maternal age and the interaction between diet

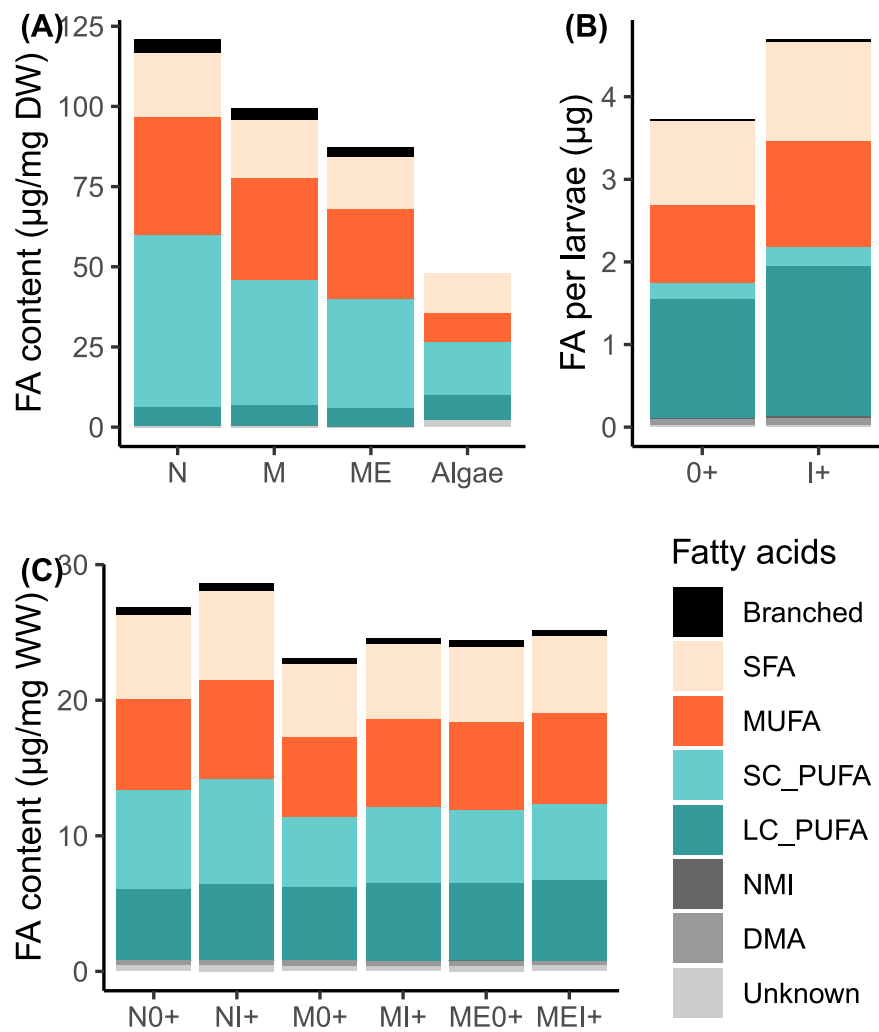


Fig. 2. Average fatty acid (A) concentration in diets fed to *Palaemon serratus* larvae (N: nauplii, M: unenriched metanauplii, ME: metanauplii enriched with microalgae), (B) total content in hatchling larvae from young (0+) and old (I+) females, and (C) concentration in juveniles according to larval diet and female age. Fatty acids are grouped into categories by differentiating between short- and long-chain polyunsaturated fatty acids (SC_PUFA<20 and LC_PUFA>20 carbons). The composition is presented (A) relative to dry weight, (B) as total amount per larva or (C) relative to wet weight. Unidentified fatty acids are grouped as Unknown.

Table 3
Relative FA composition (%) of *Palaemon serratus* larvae at hatching from young (0+) and old (I+) females. Results are summarised by FA category and FAs accounting for more than 1 % of the total in at least 1 sample are presented.

| | 0+ | I+ |
|-----------------|--------|--------|
| '14:0 | 2.6 % | 2.8 % |
| '16:0 | 16.4 % | 15.4 % |
| '18:0 | 5.7 % | 5.0 % |
| 16:1n-7 | 3.8 % | 4.6 % |
| 18:1n-7 | 5.9 % | 6.8 % |
| 18:1n-9 | 12.9 % | 12.9 % |
| 18:2n-6 | 2.9 % | 2.5 % |
| 18:3n-3 | 1.4 % | 1.3 % |
| 20:2n-6 | 1.1 % | 1.1 % |
| ARA | 5.0 % | 5.1 % |
| EPA | 18.0 % | 18.8 % |
| DHA | 11.6 % | 10.7 % |
| Totals | | |
| Branched | 0.8 % | 0.7 % |
| SFA | 27.0 % | 25.4 % |
| MUFA | 25.4 % | 23.6 % |
| PUFA | 43.9 % | 42.2 % |
| NMI | 0.4 % | 0.5 % |
| DMA | 2.0 % | 1.8 % |
| Unknown | 0.5 % | 0.5 % |

and maternal age affected the duration of larval development (Fig. 3B and S2; Table 5). At 14 and 18 °C, the duration of development decreased with temperature and with maternal age (56.79 ± 1.55 and 53.31 ± 1.43 % at 14 °C and 31.82 ± 0.84 and 29.84 ± 0.52 % at 18 °C, respectively for 0+ and I+ female larvae respectively, ±S.E.). Under the same thermal condition, larvae fed the N diet developed faster than those fed the M and ME diet (comparing N to M and ME combined, respectively 54.00 ± 1.62 and 55.58 ± 1.05 days at 14 °C, 29.69 ± 0.76 and 31.40 ± 0.74 days at 18 °C and 20.44 ± 0.13 and 25.38 ± 0.1 days at 22 °C, ±S.E.).

The relative frequency of larvae developing through the zoea 3 and zoea 3' stages varied with the interaction between temperature and female age, but not with the interaction between temperature, female age and diet (Table 4; Fig. 4). Developmental pathways including the zoea 3' stage represented 2.9 % for larvae from young females and 41.0 % for larvae from old females.

3.4. Juvenile weight and fatty acid composition

The interaction between temperature, diet, maternal age and developmental time affected weight at metamorphosis (Fig. 5; Table 6 and S3). Under the same condition (temperature and diet), the average weight of the juveniles of 0+ and I+ females were not different, except

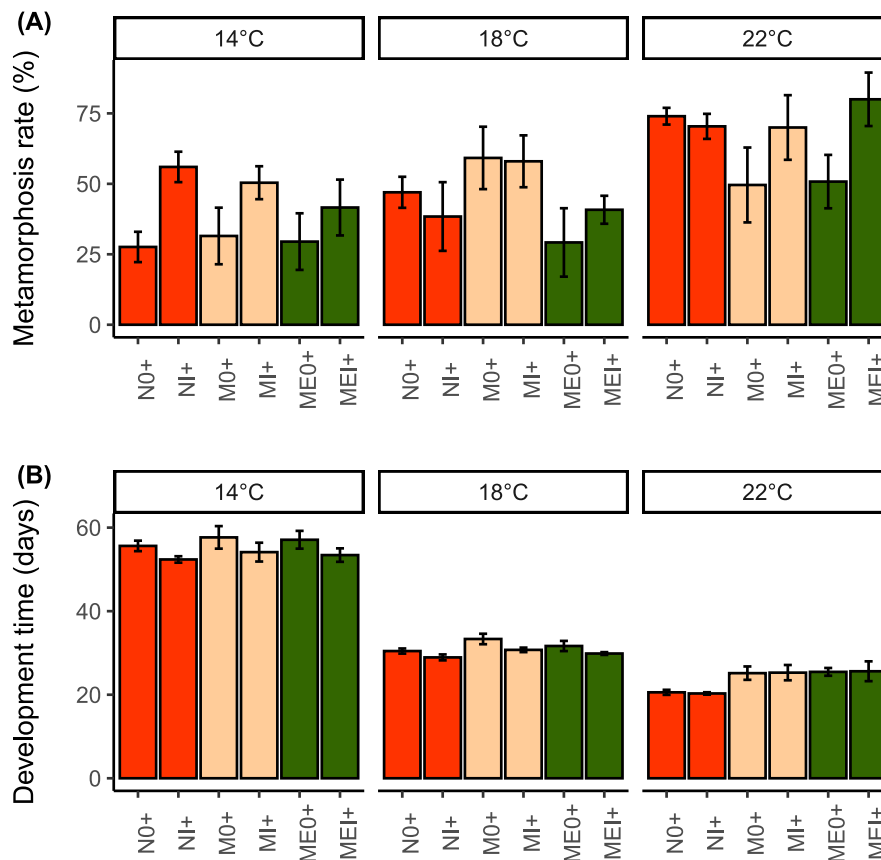


Fig. 3. (A) Rate of metamorphosis and (B) development time of *Palaemon serratus* larval brood from 5 young (0+) and 5 old (I+) females incubated at 14, 18 and 22 °C with 3 *Artemia* diets (N: hatched nauplii in red, M: unfed metanauplii in beige, ME: metanauplii enriched with microalgae in green). The ± S.E. are the deviation of the average of each brood from the overall average (n = 5 broods per condition). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 4

ANOVA results of the analysis of the effects of temperature, diet and maternal age on the rate of metamorphosis and the proportion of larvae developing through the zoea 3 and 3' in the broods of *Palaemon serratus*.

| Variable | Factor | df | Deviance Resid. | P-value |
|--------------------|-----------------------|-----------------|-----------------|---------------------|
| Metamorphosis rate | Temperature (T) | 2 | 258.81 | < 10 ⁻³ |
| | Diet (D) | 2 | 21.29 | 0.402 |
| | Age (A) | 1 | 94.45 | < 10 ⁻³ |
| | T x D | 4 | 69.41 | < 10 ⁻³ |
| | T x A | 2 | 34.78 | < 10 ⁻³ |
| | D x A | 2 | 11.12 | 0.457 |
| | T x D x A | 4 | 24.93 | < 10 ⁻³ |
| | Proportion of zoea 3' | Temperature (T) | 2 | 56.32 |
| Diet (D) | | 2 | 66.82 | < 10 ⁻¹⁵ |
| Age (A) | | 1 | 762.18 | < 10 ⁻¹⁶ |
| T x D | | 4 | 9.42 | 0.05 |
| T x A | | 2 | 29.83 | < 10 ⁻⁷ |
| D x A | | 2 | 2.56 | 0.28 |
| T x D x A | | 4 | 9.57 | 0.05 |

for the larvae fed with ME at 22 °C (3.61 ± 0.08 and 3.31 ± 0.08 respectively for 0+ and I+ females, average ± S.E.; Fig. 3C). The average weight at metamorphosis decreased with temperature (4.31 ± 0.11 , 4.29 ± 0.13 and 3.67 ± 0.13 mg respectively at 14, 18 and 22 °C, average ± S.E.) and was lower for larvae fed M and ME than for those fed N (3.81 ± 0.11 , 4.03 ± 0.19 and 4.44 ± 0.12 mg respectively, average ± S.E.). The average weight of juveniles fed the ME diet was higher than that of juveniles fed the M diet at 14 and 18 °C (4.03 ± 0.12 and 3.92 ± 0.09 mg for juveniles fed M and 4.31 ± 0.1 and 4.32 ± 0.15

Table 5

ANOVA results of the analysis of the effects of temperature, diet and maternal age on development time of the broods of *Palaemon serratus*.

| Variable | Factor | numDF | denDF | F-value | P-value |
|------------------|-----------------|-------|-------|---------|--------------------|
| Development time | Temperature (T) | 2 | 2180 | 9444.68 | < 10 ⁻³ |
| | Diet (D) | 2 | 2180 | 10.6 | < 10 ⁻³ |
| | Age (A) | 1 | 8 | 4.03 | 0.027 |
| | T x D | 4 | 2180 | 19.46 | < 10 ⁻³ |
| | T x A | 2 | 2180 | 44.64 | < 10 ⁻³ |
| | D x A | 2 | 2180 | 6.63 | 0.001 |
| | T x D x A | 4 | 2180 | 1.24 | 0.291 |

for those fed ME, at 14 and 18 °C respectively), but not at 22 °C. Within the same condition, juvenile weight increased with developmental time, more so for larvae from old females than for those from young females at 14 and 18 °C, and more so with the N diet than with the M and ME diets (Fig. 5).

The relative composition of fatty acid categories was similar for all juveniles, but those that ate N contained more fatty acids than those that ate M and ME (Fig. 2C; Table 7). The relative fatty acid composition (those present >1 % in at least one sample) of juveniles at metamorphosis varied with the interaction between temperature and diet during the larval phase and with female age class, but not with the duration of larval development (Table 8; Fig. 6). The more larvae were incubated in cold water, the more fatty acids the juveniles contained, particularly essential fatty acids (Fig. 6A and B). Larvae fed M and ME diets became juveniles richer in EPA, DHA and ARA (Fig. 6A and C). The juveniles of older females contain more fatty acids, particularly essential fatty acids, than those of young females (Fig. 6A and D).

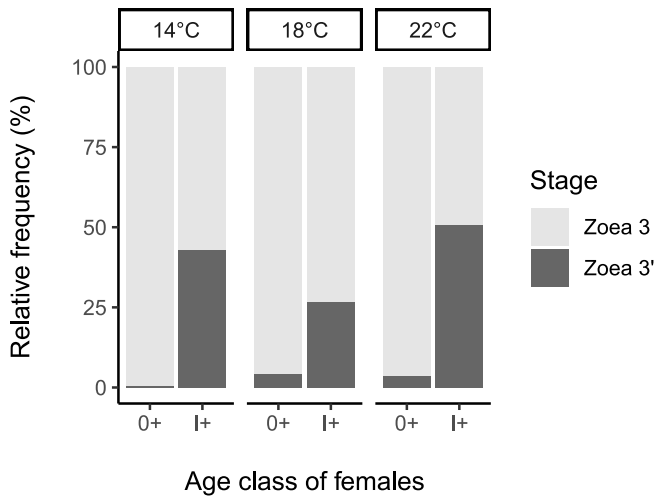


Fig. 4. Relative frequency of *Palaemon serratus* larvae developing through the zoea 3 and zoea 3' stages in relation to the age of the females (0+ and I+) that laid them and the temperature at which they were incubated (14, 18 and 22 °C). For broods from 0+ females, n = 431, 485 and 541 larvae at 14, 18 and 22 °C respectively. For broods from I+ females, n = 614, 507 and 626 larvae at 14, 18 and 22 °C respectively.

4. Discussion

Here, the interaction of temperature, prey quality and the quantity of resources transmitted to the larvae by the females affected their performance. We observed the effects of this interaction on larval

Table 6

ANOVA results of the analysis of the effects of temperature, diet, maternal age and development time on metamorphosis weight of *Palaemon serratus* juveniles.

| Variable | Factor | numDF | denDF | F-value | P-value |
|----------------|-----------------|--------|--------|--------------|--------------------|
| Weight | Temperature (T) | 2 | 2164.8 | 0.1 | 0.900 |
| | Diet (D) | 2 | 2164.3 | 9.6 | < 10 ⁻³ |
| | Age (A) | 1 | 213.8 | 27.9 | < 10 ⁻³ |
| | Time (Ti) | 1 | 2170.0 | 179.7 | < 10 ⁻³ |
| | T x D | 4 | 2164.3 | 2.3 | 0.053 |
| | T x A | 2 | 2164.8 | 4.5 | 0.011 |
| | T x Ti | 2 | 2164.8 | 8.5 | < 10 ⁻³ |
| | D x A | 2 | 2164.3 | 3.5 | 0.030 |
| | D x Ti | 2 | 2164.8 | 24.0 | < 10 ⁻³ |
| | A x Ti | 1 | 2170.0 | 42.4 | < 10 ⁻³ |
| | T x D x A | 4 | 2164.3 | 3.5 | 0.008 |
| | T x D x Ti | 4 | 2165.3 | 3.2 | 0.012 |
| | T x A x Ti | 2 | 2164.8 | 8.0 | < 10 ⁻³ |
| | D x A x Ti | 2 | 2164.8 | 4.1 | 0.016 |
| T x D x A x Ti | 4 | 2165.3 | 3.9 | 0.003 | |

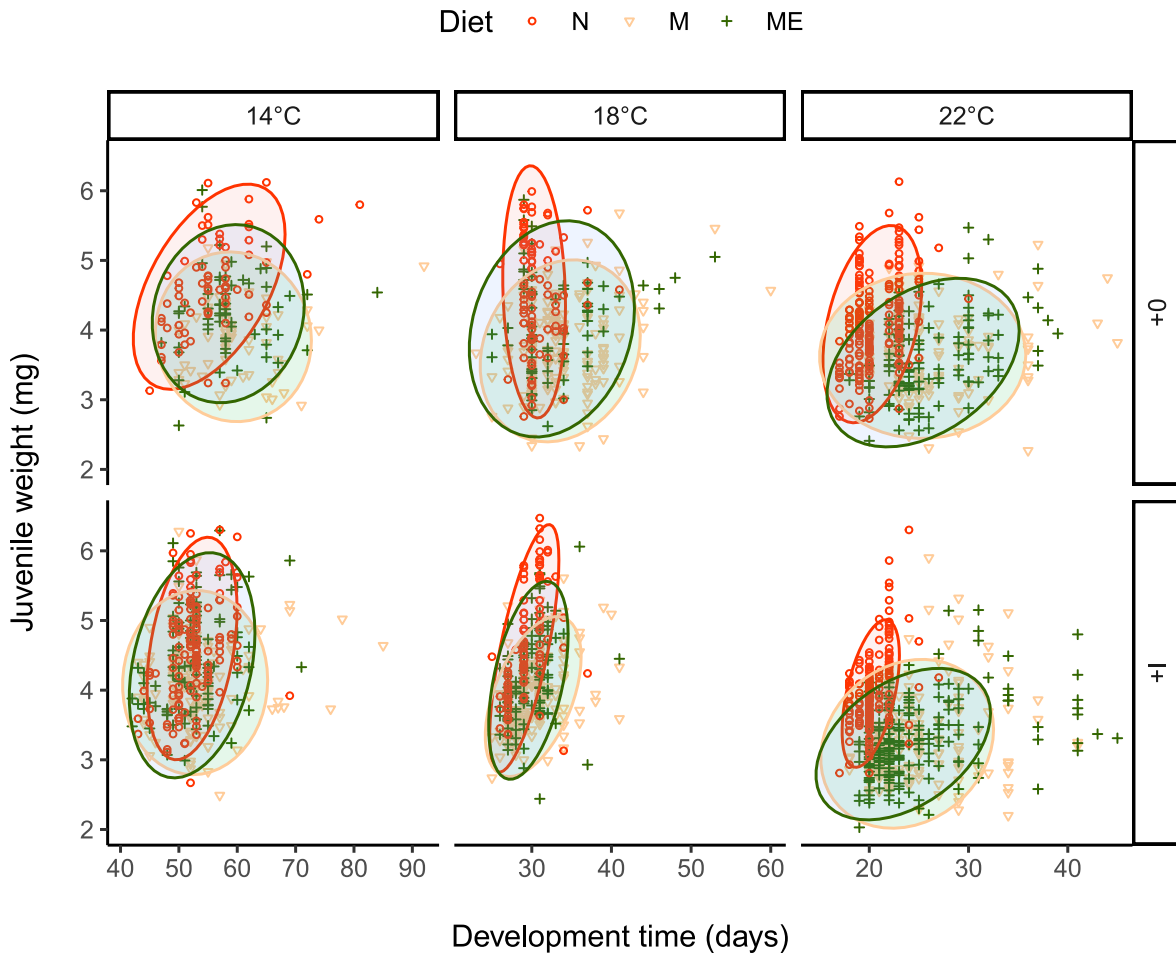


Fig. 5. Weight at metamorphosis of *Palaemon serratus* juveniles from 5 young (0+) and 5 old (I+) females according to their development time at 14, 18 and 22 °C with 3 *Artemia* diets (N: hatched nauplii in red circles, M: unfed metanauplii in beige triangles, ME: metanauplii with microalgae in green crosses). The ellipses cover 95 % of the points. For juveniles from broods of 0+ females, n = 69, 63 and 59 at 14 °C; n = 94, 148 and 73 at 18 °C and n = 185, 124 and 127 at 22 °C, with N, M and ME respectively. For juveniles from broods of I+ females, n = 140, 126 and 104 at 14 °C; n = 96, 145 and 102 at 18 °C and n = 176, 175 and 200 at 22 °C, with N, M and ME respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 7

Relative FA composition (%) of *Palaemon serratus* juveniles from young (0+) and old (I+) females after larval development with different diets (N: nauplii, M: unenriched metanauplii, ME: metanauplii enriched with microalgae). Results are summarised by FA category and FAs accounting for more than 1 % of the total in at least 1 sample are presented.

| | N0+ | NI+ | M0+ | MI+ | MEO+ | MEI+ |
|-----------------|--------|--------|--------|--------|--------|--------|
| 16:0 | 11.6 % | 11.3 % | 11.5 % | 11.1 % | 11.3 % | 11.0 % |
| 17:0 | 0.9 % | 0.9 % | 1.0 % | 1.0 % | 1.0 % | 1.0 % |
| 18:0 | 8.8 % | 9.1 % | 8.8 % | 8.6 % | 8.8 % | 8.9 % |
| 16:1n-7 | 1.0 % | 1.0 % | 1.0 % | 1.0 % | 1.0 % | 1.0 % |
| 18:1n-7 | 8.5 % | 8.5 % | 9.3 % | 9.4 % | 9.7 % | 9.6 % |
| 18:1n-9 | 13.9 % | 14.0 % | 13.8 % | 14.3 % | 14.2 % | 14.3 % |
| 18:2n-6 | 5.4 % | 5.4 % | 4.7 % | 4.8 % | 4.7 % | 4.7 % |
| 18:3n-3 | 20.1 % | 20.2 % | 16.4 % | 16.8 % | 16.0 % | 16.1 % |
| 18:4n-3 | 1.1 % | 1.2 % | 0.9 % | 1.0 % | 0.9 % | 0.9 % |
| 20:3n-3 | 2.0 % | 2.1 % | 1.4 % | 1.4 % | 1.3 % | 1.4 % |
| 20:4n-3 | 1.3 % | 1.3 % | 1.0 % | 1.1 % | 1.0 % | 1.0 % |
| ARA | 2.4 % | 2.4 % | 3.3 % | 3.3 % | 3.4 % | 3.4 % |
| EPA | 11.9 % | 11.9 % | 15.4 % | 15.0 % | 15.3 % | 15.2 % |
| DHA | 0.8 % | 1.0 % | 1.0 % | 1.1 % | 1.2 % | 1.3 % |
| 18:ODMA | 1.3 % | 1.0 % | 1.6 % | 1.1 % | 1.4 % | 1.1 % |
| Totals | | | | | | |
| Branched | 2.0 % | 1.9 % | 1.9 % | 1.9 % | 1.9 % | 1.8 % |
| SFA | 23.0 % | 22.7 % | 23.2 % | 22.4 % | 22.9 % | 22.6 % |
| MUFA | 25.2 % | 25.4 % | 25.7 % | 26.4 % | 26.5 % | 26.7 % |
| SC-PUFA | 27.0 % | 27.0 % | 22.3 % | 22.9 % | 21.8 % | 21.9 % |
| LC-PUFA | 19.6 % | 20.1 % | 23.4 % | 23.5 % | 23.6 % | 23.9 % |
| DMA | 1.6 % | 1.2 % | 1.8 % | 1.3 % | 1.6 % | 1.3 % |

Table 8

PERMANOVA results of the analysis of the effects of temperature, diet, maternal age and development time on fatty acid composition of *Palaemon serratus* juveniles (FAs accounting for more than 1 % of the total in at least 1 sample are presented).

| Factor | DF | F-value | P-value |
|-----------------|----|---------|--------------------|
| Temperature (T) | 1 | 10.82 | < 10 ⁻³ |
| Diet (D) | 2 | 34.65 | < 10 ⁻³ |
| Age (A) | 1 | 7.26 | < 10 ⁻² |
| Time (Ti) | 1 | 2.86 | 0.06 |
| T x D | 2 | 5.42 | < 10 ⁻² |
| T x A | 1 | 2.3 | 0.11 |
| T x Ti | 1 | 0.17 | 0.87 |
| D x A | 2 | 0.85 | 0.45 |
| D x Ti | 2 | 0.34 | 0.86 |
| A x Ti | 1 | 2.82 | 0.08 |

development, in terms of survival, duration and growth, and these responses were intimately linked. Under optimal conditions, i.e. at 22 °C with *Artemia* nauplii, larval survival to metamorphosis was around 75 %. Survival decreased with decreasing temperature and prey quality. The larvae produced by I+ females, which were larger and had more fatty acid reserves at hatching, survived better than those produced by 0+ females under the same incubation conditions. These maternal effects were just as observable at 22 °C with diets less concentrated in fatty acids (M and ME) as in cold water at 14 °C. The survival of larvae from I+ females was higher than that of larvae from 0+ females. The correlation between larval biomass and survival is known in decapod larvae (Giménez and Anger, 2001; González-Ortegón and Giménez, 2014; Oliphant et al., 2014). The reduction in the quality of prey when temperatures were high (22 °C) has led to nutritional stress conditions which have resulted in survival rates for larvae from 0+ females. This could be due to an increase in metabolism that can no longer be covered by food (Ravi and Manisseri, 2012; Leiva et al., 2022), since energy requirements were greater because of an increased metabolism (Fitzgibbon, 2012; Paul, 1983). Temperature determines the feeding activity of organisms and their metabolism (Ravi and Manisseri, 2012; Leiva et al., 2022; Tills et al., 2022) and the negative effects of low food availability may be mitigated (Espinosa-Novo et al., 2023) or

exacerbated (González-Ortegón and Giménez, 2014; Torres and Giménez, 2020) by increasing temperatures.

The duration of larval development increased when the temperature fell, since the time taken for each larval moult increased physiologically (O'Connor et al., 2007; Oliphant et al., 2013). Furthermore, under the most difficult thermal conditions (i.e. 14 and 18 °C), development time was significantly longer with the poorest diets. The larvae responded plastically to stress to increase their chances of surviving to metamorphosis. This ability is reflected in the increased duration of larval development at a given temperature. The developmental plasticity of *P. serratus* larvae is known and is expressed by an increase in the number of larval moults required to reach metamorphosis (Oliphant and Thatje, 2013; Baudet et al., 2022, 2024). The exacerbation of nutritional stress on the duration of larval development with increasing temperature has been observed in other decapod species (Anger and Dawirs, 1982; Torres and Giménez, 2020) and *P. serratus* (González-Ortegón and Giménez, 2014).

The development time of larvae from I+ females was also shorter than that of larvae from 0+ females. Similarly, some authors observed a higher survival rate and slower development in large winter larvae of *P. serratus* compared to small summer larvae (González-Ortegón et al., 2013, 2015). The shortened development of I+ larvae observed here was probably explained more by the reduction in the number of instars achieved conferred by their initial biomass than by the reduction in the intermoult time (Hancock, 1998; Giménez and Torres, 2002; Giménez and Anger, 2003; Giménez et al., 2004; Paschke et al., 2004; Moland et al., 2010; Oliphant and Thatje, 2013; González-Ortegón and Giménez, 2014; Oliphant et al., 2014). This shortening of the developmental pathway conferred by the initial biomass was reflected in the proportion of larvae passing through the zoea 3' stage (pleopod buds from the 3rd instar, morphogenesis normally achieved at the next larval instar; Baudet et al., 2022). Here, large larvae from old females passed more through the 3' stage, a result consistent with that of Baudet et al. (2022) who observed more zoea 3' in large winter larvae than in small summer larvae produced by females of the same size. The greater dietary independence conferred by maternal investment may have had consequences for the larvae's bioenergetics. Indeed, larvae from old females became juveniles with a higher fatty acid content than those from young females.

The benefits of higher hatching biomass were even more apparent under stressful conditions. At 14 and 18 °C, the development time of larvae from old females was shorter than that of larvae from young females, so the difference in hatching weight was compensated for. At 14 °C, the survival of I+ female larvae was higher than that of 0+ female larvae. This was also the case at 22 °C when the larvae were fed the two lowest fatty acid diets (M and ME). These results are consistent with those of González-Ortegón and Giménez (2014) showing an abbreviation of the duration of larval development of *P. serratus* correlated with the biomass at hatching under conditions of low food availability. These hatching biomass benefits can also be observed when *P. serratus* larvae are exposed to pollutants (Devineau, 1986; González-Ortegón et al., 2013, 2015). In *C. maenas*, larvae that are larger at hatching have a greater capacity for thermal attenuation of low salinity stress (Šargač et al., 2021, 2022). Older *P. serratus* females optimize the fitness of their offspring through their investment and this may explain the early winter brood of old females of *P. serratus* (Campillo, 1979; Baudet et al., 2023b). Although the larvae of this species can respond to food and thermal stresses by prolonging their larval moult, they are not able to moult to the second instar without sufficient food. This suggests that the planktonic prey available at the time of hatching of the earliest larvae covers their energy requirements.

The plastic response of development had consequences for larval growth. Although the rate of larval growth increased with temperature, the decrease in development time resulted in smaller juveniles (Dawirs et al., 1986; Anger, 1987a, 1998). The increase in temperature and diet quality each decreased the developmental time and these two factors

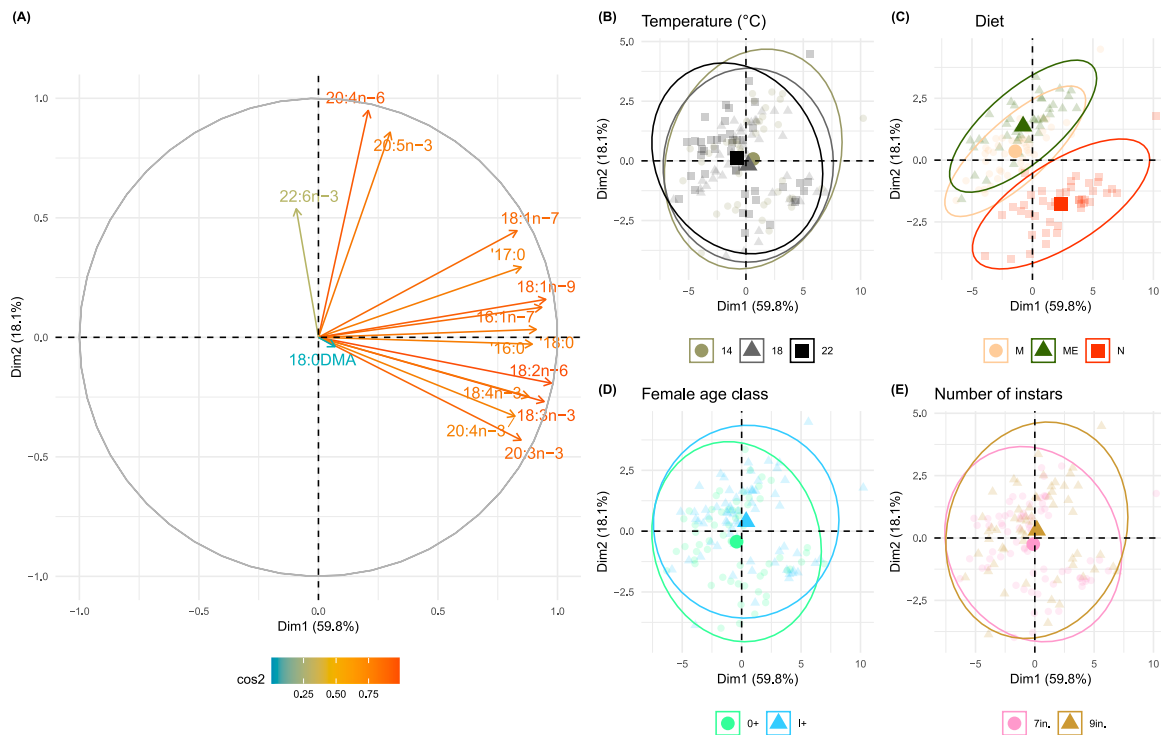


Fig. 6. Results of Principal Component Analysis (PCA) applied on fatty acid composition of *Palaemon serratus* juveniles (i.e. 131 pools of juvenile). (A) Correlation circle between fatty acids variables (fatty acids accounting for more than 1 % of the total in at least 1 sample) and the two first principal components (Dim1 and Dim2). (B–E) Location of *Palaemon serratus* juveniles pools (transparent dots), centroids (full dots) and dispersions around centroids as a function of qualitative factors (ellipses). The ellipses represent the average distance of juveniles from the centroids of the groups with a 95 % confidence interval. (B) larval incubation temperature; (C) diet (N: hatched nauplii, M: unfed metanauplii, ME: metanauplii with microalgae); (D) female age class; (E) number of instars performed.

have combined effects since larvae fed with N have a growth rate that increased as temperature increased. Under these conditions, N diet seemed to meet the increasing metabolic requirements. N reduced the duration of larval development while increasing the average weight at metamorphosis, such phenomena are known to be negatively correlated in decapods (Giménez and Torres, 2002; Oliphant et al., 2013; Leiva et al., 2022). The decrease in moulting frequency with increasing temperature in *Palaemon elegans* (a species close to *P. serratus*) caused a decrease in polyunsaturated fatty acid content (Maia et al., 2022). In the same way, the negative effects of low food availability on the development time and growth of *Hyas araneus*, *P. serratus* and *Carcinus maenas* are exacerbated by increasing temperature (Anger and Dawirs, 1982; González-Ortegón and Giménez, 2014; Torres and Giménez, 2020). Under these conditions food inputs no longer meet the increasing metabolic needs. This illustrates the high plasticity of larval development in *P. serratus* which allows for increased survival at the expense of developmental speed under stressful trophic conditions.

As the three diets did not differ in their relative fatty acid composition, the dietary stress induced here by the M and ME diets could be related to total fatty acid content, other nutritional characteristics such as protein, or the difference in prey size. The amount of food ingested by the larvae determines the number of larval moulting cycles and the rate of morphogenesis between them (Anger, 1987a; González-Ortegón and Giménez, 2014). Similar results are observed on *Homarus americanus* larvae when comparing a diet of *Artemia* nauplii with a diet of frozen adult *Artemia* (Snyder and Chang, 1986; Fiore and Tlustý, 2005). The metanauplii that were fed the microalgae mixture (ME) during 24 h were expected to become enriched in long-chain polyunsaturated fatty acids without becoming too large to be consumed by the shrimp larvae (Calado et al., 2008, 2022). Beyond triggering a plastic response in the larval developmental pathway, dietary stress caused by the M and ME diets had consequences for larval bioenergetics. Larvae fed the N diet

yielded juveniles richer in total fatty acid, but those fed the M and ME diets became juveniles richer in essential fatty acid. Similarly, the colder the temperature at which the larvae are incubated, the richer the juveniles are in fatty acids.

As expected, larvae produced by I + *P. serratus* females had a higher hatching biomass than those produced by 0+ females. Contrary to our predictions, their total fatty acid content and composition were similar. Maternal effects on the variation of lipid content at hatching in *P. serratus* are still poorly understood. González-Ortegón et al. (2018) measured a higher total lipid content in the larvae of old winter laying females than in those of young summer laying females. The fatty acid composition of the eggs could be different at laying. As reserve lipids are stored when they are in excess in the diet (Marciano et al., 2021), their composition largely reflects that of an organism's diet (Graeve et al., 1997; Antonio and Richoux, 2016; Marciano et al., 2022b). During embryonic development, crustacean eggs develop mainly by degrading the proteins and lipids present in the vitelline resources (Pandian, 1994; Anger et al., 2002). The seasonal differences could therefore be eliminated during embryonic development, as the consumption of energy reserves by embryos varies according to environmental conditions (Brillon et al., 2005; Baudet et al., 2023a). In the cold water of winter incubation, the embryos would consume more lipids (in particular polyunsaturated fatty acid and highly-unsaturated fatty acids in *P. serratus*, Narciso and Morais, 2001) which would no longer be available at hatching. In *Crangon crangon* which is also a temperate shrimp that lays eggs in different seasons, the maternal investment per egg then per larvae varies seasonally in terms of biomass but not composition (Urzúa et al., 2012; Urzúa and Anger, 2013). This seasonal difference in energy allocation per offspring, provides winter larvae with greater resistance to feeding stress (Paschke et al., 2004). It is possible that the composition of Zoea 1 is more variable between breeding years than between laying seasons (Kattner et al., 1994b), reflecting conditions (e.g.

temperature, food availability, phytoplankton bloom) during vitellogenesis and egg incubation (Viegas et al., 2012; Urzúa and Anger, 2013; Mika et al., 2014) or genetic effects (Wu et al., 2010; Tropea and Greco, 2015; Marciano et al., 2018). There is a need to study the variation in fatty acid investment to offspring during the life cycle of *P. serratus*.

Within the same decapod population, older females produce more and larger eggs (Anger and Moreira, 1998; Bilgin and Samsun, 2006; Smith and Ritar, 2007). In addition, they feed at a higher trophic level, which is reflected in the resources transmitted (González-Ortegón et al., 2018). The offspring produced by the largest females therefore generally have better fitness (Fischer et al., 2003). In decapods that reproduce several times during the breeding season before dying at the end of it, females can produce increasingly less efficient broods (Marciano et al., 2018, 2022a). Since variations in maternal investment per offspring are modulated in anticipation of the environment experienced during embryo-larval development, these mechanisms are referred to as 'adaptive maternal effects' (Marshall and Uller, 2007; Burgess and Marshall, 2011). The biomass invested per offspring is determined during ovarian maturation, a period that takes place several months before larval development (more than 4 months in winter and at least 1 month in summer in *P. serratus*). Autumn environmental conditions (reduced photoperiod and temperature) would therefore stimulate females to invest more energy per offspring, while late spring/early summer environmental conditions (increased photoperiod and temperature) would stimulate them to produce more gametes. The combination of these two factors is known to determine the trade-off between fecundity and biomass per egg in other invertebrates (i.e. Polychaeta; Olive and Pillai, 1983; Wang et al., 2020). We know that the diet of *P. serratus* females varies during their life cycle, depending on their seasonal lateral migrations and/or their change in trophic status (Forster, 1951; Campillo, 1979; González-Ortegón et al., 2018; Raoux et al., in preparation).

5. Conclusion

The results observed here support the great plastic capacity that enables carid shrimp larvae to cope with environmental stresses. They also highlighted the increase in larval performance, particularly in cold conditions, conferred by the increase in maternal investment per offspring with the age of the females, but also by the increase in the quality of the prey, highlighting the relevance of using *Artemia* nauplii to feed decapod larvae.

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CRediT authorship contribution statement

Jean-Baptiste Baudet: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Benoît Xuereb:** Writing – original draft, Supervision, Funding acquisition, Conceptualization. **Gauthier Schaal:** Writing – original draft, Supervision, Conceptualization. **Marc Rollin:** Methodology. **Agnès Poret:** Investigation. **Léa Jeunet:** Investigation. **Enora Jaffrézic:** Investigation. **Aurélié Dufлот:** Investigation. **Thibault Charles:** Investigation. **Frank Le Foll:** Supervision. **Romain Coulaud:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial

interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jtherbio.2024.103796>.

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