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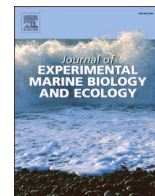
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## Seasonal and age-related variations in egg biomass and fatty acid composition of the common prawn *Palaemon serratus*

Jean-Baptiste Baudet<sup>a</sup>, Benoît Xuereb<sup>a</sup>, Gauthier Schaal<sup>b</sup>, Marc Rollin<sup>a</sup>, Agnès Poret<sup>a</sup>, Aurélie Duflot<sup>a</sup>, Léa Jeunet<sup>b</sup>, Enora Jaffrézic<sup>b</sup>, Frank Le Foll<sup>a</sup>, Romain Coulaud<sup>a,\*</sup>

<sup>a</sup> Le Havre Normandie University (ULHN), FR CNRS 3730 SCALE, UMR-INERIS 02 Environmental Stresses and Biomonitoring of Aquatic Ecosystems (SEBIO), 25 rue Philippe Lebon, 76600 Le Havre, France

<sup>b</sup> Univ Brest, CNRS, IRD, Ifremer, LEMAR, Plouzane, France

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### ABSTRACT

In crustaceans that live in seasonal environments and produce several broods during an annual cycle, there are generally seasonal patterns in reproductive traits. Thus, females are able to modulate the trade-off between per offspring investment and quantity of eggs produced in order to maximise the fitness of their offspring in response to the environmental conditions they will face during their development. We collected females of *Palaemon serratus* (Pennant, 1777) that had just laid eggs during the entire laying season from December 2021 to November 2022 on the coast of Seine-Maritime (France). We measured their fecundity, biomass per egg and the fatty acid composition of the eggs. The largest females laid their eggs from December to March (“winter laying”) and from May to July (“summer laying”), while the smallest females laid from January to August. Fecundity and in general biomass per egg increased with the size of the females. The FA concentration of eggs decreased throughout the laying season and winter eggs were more concentrated in essential PUFAs than summer eggs. In summer, the old females laid eggs with the same biomass as those laid by the young females, enabling them to significantly increase their relative fecundity. All these trends are consistent with the environmental conditions encountered by future embryos and larvae. These results provide a clear illustration of the maternal effects and trade-offs between reproductive traits observed in decapods.

### 1. Introduction

In marine invertebrates with highly seasonal environments, the various events linked to reproduction and the development of the next generation can take place under drastically different environmental biotic and abiotic conditions. For example, temperature is a well-known highly variable environmental parameter that influences the reproduction of marine invertebrates. (Tills et al., 2022; Baudet et al., 2023; Baudet et al., 2024). Food also plays a central role in the reproduction of marine invertebrates and varies considerably throughout the year (Baudet et al., 2024). When mothers modulate the phenotype of their offspring in anticipation of the environment to which it will be subjected, we refer to maternal effects (Marshall and Uller, 2007; Burgess and Marshall, 2011). As a general rule, the more maternal energy offspring receive, the higher their fitness will be, whatever the environmental conditions encountered (Fischer et al., 2003). In egg-bearing decapod species, female size and egg number are correlated due to the

size of the incubating cavity between the carapace and the pleopods (Hines, 1982; Bilgin and Samsun, 2006; Smith and Ritar, 2007). In addition to affecting total reproductive output, the size of female is correlated with the average egg biomass (Corey and Reid, 1991; Reid and Corey, 1991; Clarke, 1993; Anger and Moreira, 1998). However, the relationship between the number of eggs and the size of the female may vary during the breeding season (Urzúa et al., 2012).

Decapods that reproduce several times a year display seasonality in their reproductive traits (Bas et al., 2007; Vázquez et al., 2013; Guzmán et al., 2016; Hamasaki et al., 2021; Marciano et al., 2022a). Females produce fewer large eggs during the harshest period of the breeding season than during the most favourable period (“winter eggs versus summer eggs”, Havinga, 1930; Boddeke, 1982; Paschke, 1998). The larger winter eggs give birth to larger larvae that are more resistant to environmental stresses (Paschke et al., 2004; Espinoza et al., 2016). Seasonal variations in the maternal investment per offspring therefore follow environmental variations such as temperature and availability of

\* Corresponding author.

E-mail address: [romain.coulaud@univ-lehavre.fr](mailto:romain.coulaud@univ-lehavre.fr) (R. Coulaud).

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planktonic resources during the larval phase, with larger larvae as the beginning of the breeding season, when temperature and food availability are less favourable (Pond et al., 1996; Jónasdóttir and h., 1999; Urzúa et al., 2012; Urzúa and Anger, 2013; Seguel et al., 2019).

In addition to seasonally modulating the egg biomass, crustacean females are able to modulate the egg reserves composition (Amsler and George, 1984; Fischer et al., 2009; Urzúa et al., 2012; Bascur et al., 2017). During embryonic and larval development, crustacean eggs develop mainly by relying on yolk proteins and lipids (Pandian, 1994; Anger et al., 2002; Brillon et al., 2005). Among lipids, phospholipids are essential structures of membrane cells, notably with regard to membrane fluidity 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 (FAs) fulfil these two roles depending on their length and unsaturation level (Parzanini et al., 2023). Polyunsaturated fatty acids (PUFAs), and especially long-chain PUFAs, are crucial to the development of decapods at embryonic (Narciso and Morais, 2001; Morais et al., 2002; Sato and Suzuki, 2010) and larval stages (Kanazawa et al., 1985; Mourente and Rodríguez, 1997). The FAs of polar lipids contribute to regulate the fluidify cell membranes, especially in cold water (Chapelle, 1986; Harwood, 1988; Sargent 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; Giménez and Anger, 2001; Tully et al., 2001; Smith and Ritar, 2007; Fischer et al., 2009; Emmerson et al., 2017).

The common prawn, *Palaemon serratus* (Pennant, 1777), is a European shrimp of high ecological (Atrill and Thomas, 1996; Sá et al., 2006; Sturbois et al., 2022) and commercial value (Fahy and Gleeson, 1996; FranceAgriMer, 2017; ICES, 2022). Its lifespan ranges from 2 to 5 years and shows a strong sexual dimorphism (Sollaud, 1916; Cole, 1958; Forster, 1959). From December to March, females breed and incubate their eggs in deeper habitats than in summer (Guerao and Ribera, 2000). The laying frequency of females varies with latitude, from once a year in Ireland to three times a year in France (Cole, 1958, in Haig et al., 2014). The age of the females also determines their annual laying frequency, with 1 laying for females in their first year of life (cohort 0+) and 2 laying in older females (winter and summer laying, Campillo, 1979). Older females (cohort II+ or more) might be able to lay a third time according to Cole (1958) and Campillo (1979). Although this life cycle seems to be well known, the periods of each reproductive event are wide and overlapping (Campillo, 1979). Few authors have studied the variations in reproductive traits of *P. serratus* according to the age of the females and the laying season. Huxley (2011), Emmerson et al. (2017) and González-Ortegón and Giménez (2014) measured an increase in fecundity and offspring size with female size (and thus age) but did not study the effect of laying season. González-Ortegón et al. (2018) measured differences in size and lipid content between offspring produced by large winter females and small summer females. Therefore, they could not separate the female size effect from the season effect. In a recent work, we measured differences in size between larvae produced by winter and summer females of the same size (Baudet et al., 2022). Despite these few studies, little is known about the variation in reproductive traits of *P. serratus* during its life cycle.

The objectives of the present study on *P. serratus* are (i) to better understanding the phenology of laying periods of this species according to the size of the females before to characterise variations in (ii) fecundity, (iii) egg biomass and (iv) fatty acid composition of energetic reserves transmitted by mothers. We expect that as the females of this species age, they produce more, larger and richer eggs. We hypothesise that reproductive traits also vary with the seasons, with few large and rich winter eggs and many small and poor summer eggs.

## 2. Materials and methods

### 2.1. Collection of egg-bearing females

To study the reproduction of *Palaemon serratus*, a maximum of 20 egg-bearing females per month were sampled between December 2021 and November 2022 on Saint-Jouin-Bruneval coastline (Seine-Maritime, France). From December to March, shrimps were harvested at a depth of about 15–20 m using professional traps, more thermally buffered habitat to which this species migrates in winter (Campillo, 1979). From April to November, sampling by hand-netting was carried out on the foreshore (Decision No. 286 / 2020, Interregional Directorate of the Sea Eastern Channel-North Sea). As egg biomass and composition change during embryonic development (Richard, 1974; Wehrmann and Albornoz, 1998; Wehrmann and Kattner, 1998; Anger et al., 2002), only females carrying eggs in the early stages of development were sampled. Richard (1974) proposed a division of embryonic development into 9 stages (from A to H') and we selected only females carrying eggs in the first 3 stages (A, B and C). In the stage A, the eggs are completely filled with dark green or reddish-brown vitellus. In the stage B, the translucent germinal disc is visible and extends to less than a quarter of the egg's perimeter. In the stage C, the embryo occupies one quarter to one half of the perimeter of the egg. The total length (from rostrum to telson) and cephalothorax length (from the tip of the rostrum to the posterior dorsal edge of the cephalothorax) of each female were measured.

### 2.2. Estimating the age of females

As the hard parts are replaced during the moult, it is difficult to estimate the age of the crustaceans (Smith and Addison, 2003; Bosley and Dumbauld, 2011; Rebert, 2019). The age of *P. serratus* females can be determined using the size (cephalothorax length) - age (annual cohort) relationship of Campillo (1979). The shrimp collected were therefore classified by age cohort, belonging to cohort year 0+ with size of cephalothorax (17–34 mm), I+ (35–46 mm), II+ (47–49 mm) and III+ (over 50 mm). Within the 0+ cohort, shrimp from the previous year's winter spawning (28–34 mm) were differentiated from those from the previous year's summer spawning (17–28 mm), since their metamorphosis as juveniles was 2 to 4 months apart Campillo (1979).

### 2.3. Total clutch weight, fecundity and average egg weight

All eggs were removed from the females with fine forceps and rinsed with distilled water. For each clutch, the total clutch weight and the fresh weight of 100 eggs were measured. The absolute average egg weight of each clutch was calculated from the weight of 100 eggs. The absolute fecundity of each female, i.e. the number of eggs attached to its pleopods, was calculated by dividing the total clutch weight by the average egg weight (Bas et al., 2007; Urzúa et al., 2012). The average relative egg weight and relative fecundity are the absolute values divided by the length of the female (Vázquez et al., 2013).

### 2.4. FA content analysis

The total FA content and composition of clutches sampled from December to July were measured after they had been frozen at  $-80\text{ }^{\circ}\text{C}$  then freeze-dried for 24 h. Given that embryos consume their lipid reserves as they develop (Herring, 1974; Figueiredo et al., 2008a, 2008b), only broods at the same embryonic stage (i.e. B) were analysed. 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  $80\text{ }^{\circ}\text{C}$  for 30 min, before being transmethylated by adding 1.6 mL of a MeOH-H<sub>2</sub>SO<sub>4</sub> mixture (3.4 %, v,v) and heating at  $100\text{ }^{\circ}\text{C}$  for 10 min. C23:0 was used as an internal standard for FA quantification. GC analysis was

carried out on a Varian CP8400 gas chromatograph using two separations simultaneously on a polar column (Front, ZBWAX: 30 mm × 0.25 mm ID × 0.25 μm, Phenomenex) and a non-polar column (Middle, ZB5HT: 30 m × 0.25 mm ID × 0.25 μm, Phenomenex). The temperature program used by the GC consisted of an initial heating from 60 °C to 150 °C at 50 °C.min<sup>-1</sup>, then to 170 °C at 3.5 °C.min<sup>-1</sup>, to 185 °C at 1.5 °C.min<sup>-1</sup>, to 225 °C at 2.4 °C.min<sup>-1</sup>, and finally to 250 °C at 5.5 °C.min<sup>-1</sup> and maintained for 25 min.

2.5. Statistical analysis

Statistical procedures were implemented with R software (R Core Team, 2020). Before using parametric analysis, normality and homoscedasticity were checked using the Shapiro-Wilk test and the Bartlett test, respectively. To test the effects of female length, month and embryonic stage on clutch weight, fecundity and egg weight, we used linear models including interaction terms (*lm* function). In order to have a design with several individuals in each condition, we grouped the months December and January, February and March, April and May and lastly June, July and August. To calculate the correlations between female length and clutch weight, female length and fecundity, female length and average egg weight and relative egg weight and relative fecundity, we used Spearman correlation tests (*cor.test* function). To test the effects of laying period and maternal age class on fatty acid egg 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) after transforming the data using the Hellinger method. PERMANOVA and PCA analysis included only FAs representing at least 0.5 and 1 % of the total FA composition in at least one of the samples respectively.

3. Results

3.1. Females sampled

All egg-bearing females sampled here were between 60 and 105 mm in total length (Fig. 1a). Respectively 20, 73 and 27 carried eggs in stages A, B and C (Table 1). From December 2021 to March 2022, 14 to 20 females caught in professional traps were sampled per month. In December, only females larger than 94 mm (class I+ and II+) were sampled (Fig. 1a). The II+ female caught in December was the only one

Table 1

Number of *Palaemon serratus* females sampled per month, embryonic stages and sampling method.

Date	Sampling methods	Total number of females sampled	Embryonic stage		
			A	B	C
10/12/2021	Professional traps	14	0	10	4
19/01/2022	Professional traps	20	7	11	2
10/02/2022	Professional traps	20	1	16	3
04/03/2022	Professional traps	20	2	13	5
21/04/2022	Hand-netting	9	1	7	1
03/05/2022	Hand-netting	15	3	9	3
16/06/2022	Hand-netting	18	5	5	8
15/07/2022	Hand-netting	3	1	1	1
16/08/2022	Hand-netting	1	0	1	0
12/09/2022	Hand-netting	0	0	0	0
10/10/2022	Hand-netting	0	0	0	0
10/11/2022	Hand-netting	0	0	0	0

with eggs in the early stages of development among all the females caught in the year (Fig. 1b). From April to June 2022, 9 to 18 females per month were netted on the foreshore. In April, only class 0+ females (65–77 mm) were caught. Class 0+ females from the previous year's winter laying laid eggs as early as January, while those from the summer laying laid eggs from April (Fig. 1b). Only 4 egg-bearing females were caught between July and August 2022, and none between September and November 2022.

3.2. Total reproductive investment

The total clutch weight and fecundity of the sampled females varied respectively between 113 and 820 mg for 1020 to 6129 eggs. Clutch weight varied with female length and month and their interaction, but not with embryonic stage (Table 2). Fecundity varied with the

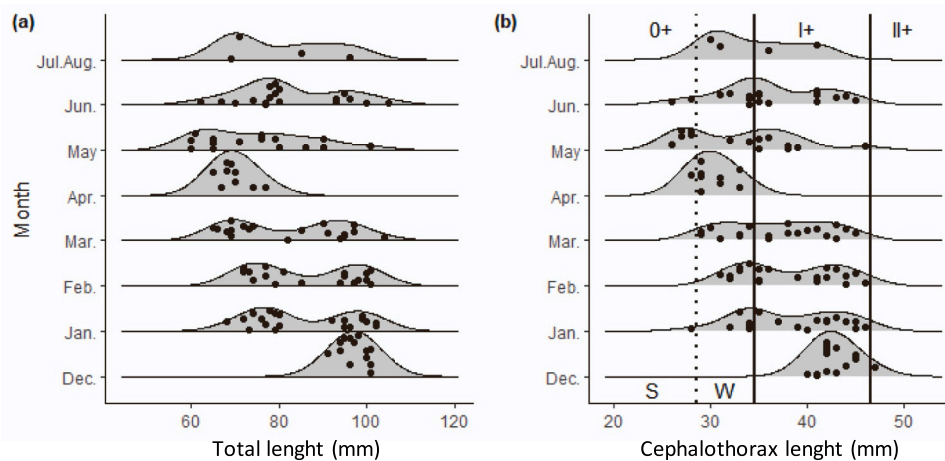


Fig. 1. Monthly relative distribution of (a) total length and (b) cephalothorax length of *Palaemon serratus* sampled females. July and August females are gathered. Each point corresponds to a sampled female. The solid vertical bars separate the 0+, I+ and II+ cohorts. The dotted vertical bar separates the 0+ cohort from the summer laying (S) from the winter laying (W) of the previous year.

**Table 2**

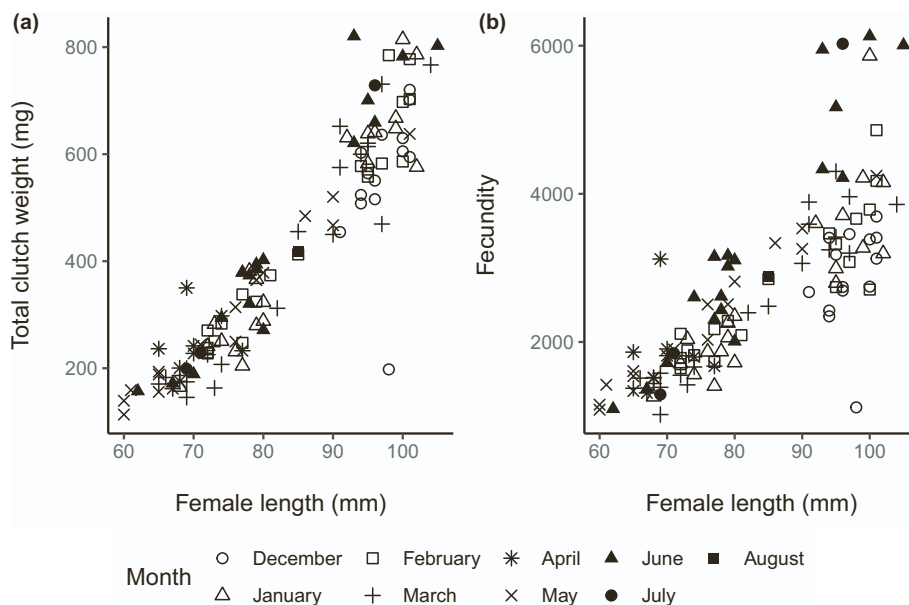
Results of the ANOVA analysing the effects of female length, month and embryonic stage on the total clutch weight, the fecundity and the average egg weight of *Palaemon serratus* females.

	Factor	df	F	P
Clutch weight	Female length (L)	1	1300.21	<0.05
	Month (M)	3	6.90	<0.05
	Embryonic stage (S)	2	1.62	0.20
	L x M	3	4.9156	<0.05
	L x S	2	0.8924	0.41
	M x S	6	0.9837	0.44
	L x M x S	6	0.7591	0.60
Fecundity	Female length (L)	1	446.01	<0.05
	Month (M)	3	29.72	<0.05
	Embryonic stage (S)	2	3.43	0.06
	L x M	3	12.81	<0.05
	L x S	2	6.29	<0.05
	M x S	6	1.03	0.41
	L x M x S	6	1.97	0.08
Egg weight	Female length (L)	1	314.01	<0.05
	Month (M)	3	27.58	<0.05
	Embryonic stage (S)	2	38.12	<0.05
	L x M	3	10.12	<0.05
	L x S	2	4.78	<0.05
	M x S	6	4.92	<0.05
	L x M x S	6	0.86	0.53

interaction of female length and month and with the interaction of female length and embryonic stage, but not with the interaction of month and embryonic stage (Table 2). Female length was correlated with clutch weight ( $\rho = 0.92, P < 10^{-16}$ ; Fig. 2a) and fecundity ( $\rho = 0.84, P < 10^{-16}$ ; Fig. 2b). Among females over 90 mm, average fecundity was  $2885 \pm 176$  eggs in December  $3645 \pm 121$  from January to May  $5405 \pm 316$  from June to July ( $\pm$  S.E.). Among females under 80 mm, the average monthly fecundity varied between  $1438 \pm 61$  and  $2347 \pm 232$  eggs ( $\pm$  S.E.), with no seasonal trend.

**3.3. Egg weight**

The average egg weight varied between 0.10 and 0.23 mg. We observed significant variations of average egg weight in relation to female size, month of the year and embryonic development stage, and the simple interactions between these different factors are significant

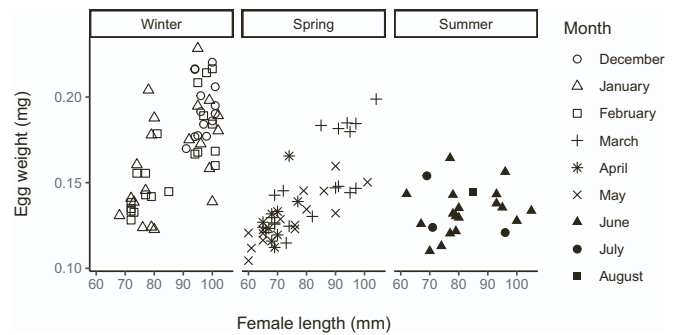


**Fig. 2.** Relationship between the length (total length from rostrum to telson) of *Palaemon serratus* females sampled from December to August and (a) their clutch weight and (b) their fecundity.

(ANOVA, Table 2; Fig. 3; Fig. S1). In general, average egg weight increases as embryonic development progresses, except in May and June when this effect is less marked (Fig. S1). At stages B and C, the average egg weight decreased during the laying season. In contrast, the average egg weight of stage A eggs didn't vary with the laying season. The average egg weight was correlated with female length in winter ( $\rho = 0.63, P < 10^{-7}$ ; Fig. 3) and spring ( $\rho = 0.81, P < 10^{-11}$ ; Fig. 3), but not in summer ( $\rho = 0.14, P = 0.53$ ; Fig. 3). Relative average egg weight and relative fecundity were negatively correlated ( $\rho = -0.47, P < 10^{-8}$ ; Fig. 4).

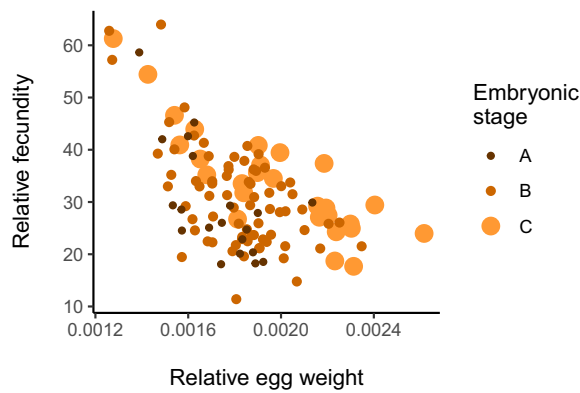
**3.4. Fatty acid composition of eggs**

Eggs were composed mainly of long-chain PUFAs ( $39.5 \pm 0.7\%$ ) with eicosapentaenoic acid (EPA, 20:5n-3) alone representing on average  $22.2 \pm 0.4\%$  of the total FA, monounsaturated FAs ( $31.9 \pm 0.4\%$ ) and saturated FAs ( $20.7 \pm 0.4\%$ ), while short-chain PUFAs represented only  $4.7 \pm 0.5\%$  of the FA pool (Table 3). FA concentration and relative composition of the different FA categories was similar between the eggs laid by class 0+, I+ and II+ females (PERMANOVA,  $p = 0.28$ ; Table 4; Fig. 5; Fig. 6). In contrast, we observed significant seasonal variations in the FA concentration and composition of the eggs. Winter females laid eggs with a higher fatty acid concentration than summer



**Fig. 3.** Relationship between the length (total length from rostrum to telson) of *Palaemon serratus* females and their average egg weight in winter, spring and summer.





**Fig. 4.** Relationship between relative average egg weight and relative fecundity (absolute values divided by the length of the female) of each sampled female *Palaemon serratus*. Dot size increases with embryonic stage.

females (mean 205.42 ± 5.62 µg/mg dry weight between December and February and 165.45 ± 7.50 between June and July). Winter eggs were more concentrated in EPA and docosahexaenoic acid (DHA, 22:6n-3) than summer eggs (respectively 44.57 ± 1.37 and 1.29 ± 0.75 µg/mg dry weight in winter and 35.18 ± 2.70 and 0.75 ± 0.08 µg/mg dry weight in summer, mean ± S.E.). Summer eggs are more concentrated in 18:2n-6 and 18:3n-3 than winter eggs (respectively 2.87 ± 1.07 and 1.46 ± 0.16 µg/mg dry weight in winter and 3.62 ± 0.56 and 4.47 ± 0.56 µg/mg dry weight in summer, mean ± S.E.).

**Table 3**

Mean relative fatty acid composition (%) of *Palaemon serratus* newly laid eggs (embryonic stage B) by females of different age classes (0+ to II+) collected throughout the breeding season (December to July). The results are summarised by FA category and FAs accounting more than 0.5 % of the total in at least 1 sample are presented.

	Dec.		Jan.		Feb.		Mar.		Apr.		Mai		Jun.		Jul.
	I+ (n = 8)	II+ (n = 1)	0+ (n = 4)	I+ (n = 5)	0+ (n = 3)	I+ (n = 6)	0+ (n = 4)	I+ (n = 5)	0+ (n = 6)	0+ (n = 6)	I+ (n = 4)	0+ (n = 2)	I+ (n = 5)	0+ (n = 1)	
'14:0	2.22 % 14.47	2.37 %	2.44 % 14.05	1.93 % 14.05	2.09 %	1.9 % 13.97	2.71 % 12.64	1.88 % 12.64	2.04 %	3 %	2.2 % 13.45	2.23 % 14.44	2.82 % 14.44	1.81 %	
'16:0	%	15.34 %	13.34 %	%	12.55 %	%	13.34 %	%	13.59 %	13.97 %	%	15.19 %	%	17.25 %	
'18:0	3.65 % 10.47	3.68 %	3.29 % 10.47	3.24 % 10.47	3.5 %	3.25 % 10.17	2.88 %	3.26 %	2.8 %	3.14 %	2.77 %	3.44 %	3.36 %	3.29 %	
16:1n-7	%	10.85 %	11.07 %	9.57 %	11.25 %	%	10.73 %	10.5 %	8.39 %	9.56 %	9.6 %	8.97 %	8.98 %	7.65 %	
17:1n-7	0.76 %	0.76 %	0.74 %	0.76 %	1.03 %	1.16 %	0.84 %	0.93 %	0.59 %	0.44 %	0.67 %	0.52 %	0.5 %	0.7 %	
18:1n-7	6.99 % 13.18	6.58 %	6.85 % 13.75	6.63 % 13.75	6.48 %	6.93 % 13.38	6.59 %	6.53 % 13.59	6.83 %	8.4 %	6.84 % 12.66	7.69 % 13.46	7.03 % 13.46	6.22 %	
18:1n-9	%	11.42 %	10.61 %	%	12.25 %	%	12.29 %	%	17.06 %	10.64 %	%	14.03 %	%	19.3 %	
18:2n-6	0.8 %	0.76 %	1.08 %	0.85 %	0.99 %	0.8 %	0.93 %	0.86 %	2.61 %	1.64 %	1.53 %	2.36 %	1.98 %	2.83 %	
18:3n-3	0.63 %	0.51 %	1.13 %	0.72 %	0.66 %	0.55 %	0.63 %	0.62 %	2.25 %	1.33 %	1.3 %	3.26 %	2.17 %	4.27 %	
18:4n-3	0.6 %	0.62 %	0.61 %	0.49 %	0.45 %	0.5 %	0.48 %	0.38 %	0.69 %	0.76 %	0.63 %	0.8 %	0.9 %	1.19 %	
ARA	2.01 % 22.02	2.34 %	2.5 % 20.57	2.29 % 20.57	2.85 %	2.39 % 21.58	2.53 %	2.48 % 21.84	4.09 %	1.67 %	2.8 % 22.58	2.46 % 22.59	2.35 % 22.59	3.28 %	
EPA	%	21.42 %	23.24 %	%	21.64 %	%	22.97 %	%	21.37 %	25.91 %	%	20.39 %	%	15.4 %	
21:5n-3	0.67 %	0.63 %	0.67 %	0.55 %	0.63 %	0.63 %	0.58 %	0.55 %	0.47 %	0.84 %	0.54 %	0.43 %	0.5 %	0.26 %	
22:5n-3	0.84 % 10.88	0.93 %	1.11 % 10.65	1.11 % 10.65	1.16 %	1.06 % 10.93	1.09 %	1.27 % 10.85	1.12 %	0.86 %	1.11 % 10.69	1 %	0.95 %	0.8 %	
DHA	%	11.27 %	9.92 %	%	10.06 %	%	10.63 %	%	6.53 %	9.12 %	%	7.98 %	8.69 %	7.63 %	
Totals															
Branched	1.16 % 21.86	1.35 %	1.41 % 20.79	1.25 % 20.79	1.42 %	1.25 % 20.85	1.15 %	1.44 % 19.49	1.05 %	0.63 %	0.97 % 19.88	0.95 %	0.92 % 21.98	0.79 %	
SFA	%	23.11 %	20.72 %	%	19.93 %	%	20.49 %	%	19.82 %	21.31 %	%	22.22 %	%	23.79 %	
MUFA	33.66	32 %	31.97 %	32.96	34.42 %	34.4 %	33.84 %	34.89	35.22 %	31.39 %	33.17	33.16 %	32.05	35.24 %	
PUFA	41.88	41.94 %	44.16 %	43.64	42.11 %	41.98	43.21 %	42.3 %	42.8 %	45.6 %	44.61	42.71 %	44 %	39.27 %	
NMI	0.49 %	0.65 %	0.74 %	0.47 %	0.84 %	0.55 %	0.45 %	0.83 %	0.2 %	0.26 %	0.48 %	0.16 %	0.22 %	0.11 %	
DMA	0.94 %	0.95 %	1 %	0.89 %	1.28 %	0.97 %	0.85 %	1.04 %	0.9 %	0.8 %	0.89 %	0.8 %	0.82 %	0.8 %	

## 4. Discussion

### 4.1. Laying period by age cohort

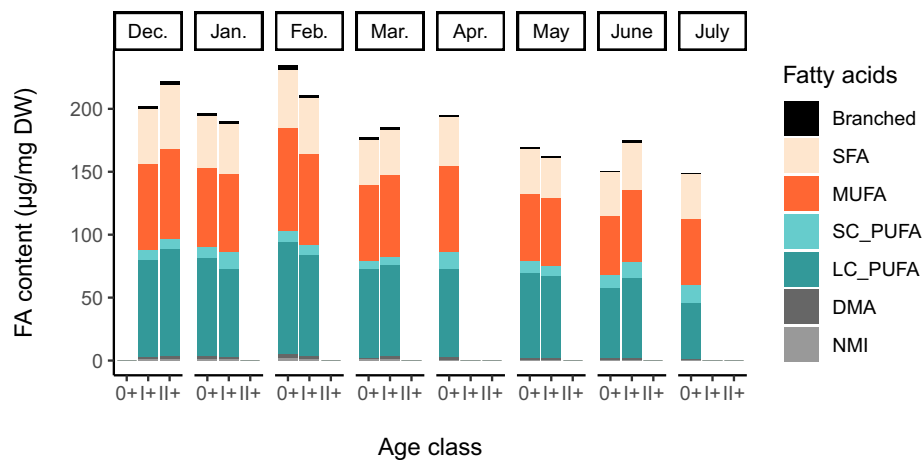
We found *Palaemon serratus* females carrying eggs in the early stages of embryonic development from December to August. These dates correspond to the laying period described by several authors (Campillo, 1979; Guerao and Ribera, 2000). At the beginning of the laying season (December), only females older than one year (I+ and II+) laid eggs. During the entire laying season, only one II+ female and no III+ carrying newly laid eggs were caught. These two cohorts represent about 2 % of the female population of *P. serratus* (Campillo, 1979). I+ females with early eggs were harvested every month between December and July except April. In March and April, we observed many I+ females in the field with eggs ready to hatch and their ovaries were in stage 4 or 5 (ready to lay a new clutch). These two results reveal that large females at our site lay their winter eggs from December to March and their summer eggs from May to July (which is consistent with Campillo, 1979).

Campillo's cohort classification was used to identify 0+ females from the previous year's winter clutch from those from the previous year's summer clutch. The 0+ females born from the previous winter laying laid their eggs from January to July, while those from the summer laying (60 to 67 mm total length) were only observed and collected from April

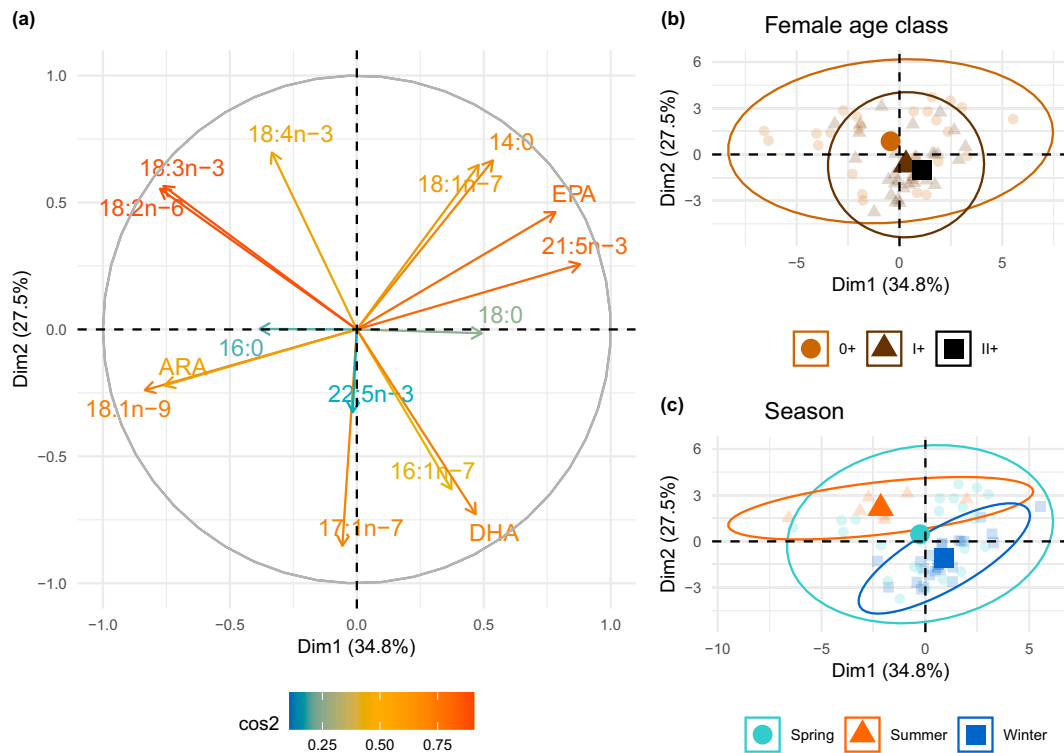
**Table 4**

PERMANOVA results of the analysis of the effects of laying month and age class on fatty acid composition of *Palaemon serratus* eggs (FAs accounting for more than 0.5 % of the total in at least 1 sample are presented).

Factor	df	F	P
Month (M)	7	5.95	<0.05
Age class (A)	2	1.41	0.28
M x A	4	0.85	0.84



**Fig. 5.** Mean fatty acid composition (relative to dry weight) of newly laid *Palaemon serratus* eggs (embryonic stage B) by females of different age classes (0+ to II+) collected throughout the breeding season (December to July). The FAs were grouped into categories by differentiating between short-chain and long-chain PUFAs (SC\_PUFA <20 and LC\_PUFA >20 carbons). The numbers of broods analysed are shown in Table 3.



**Fig. 6.** Results of principal component analysis (PCA) applied to the fatty acid composition of *Palaemon serratus* egg clutches after Hellinger transformation. (a) Correlation circle between fatty acid variables (FA representing more than 1 % of the total in at least 1 sample) and the first two principal components (Dim1 and Dim2). (b-c) Location of clutches (transparent dots), centroids (solid dots) and dispersions around centroids as a function of qualitative factors (ellipses). (b) age class of females; (c) laying season. The ellipses represent the average distance of the clutches from the centroids of the groups with a 95 % confidence interval. FAs accounting more than 1 % of the total in at least 1 sample are presented.

to June. These individuals had recently reached the first maturity size of the species, i.e. 55 mm after 9–10 months of juvenile life (Forster, 1951; Fahy et al., 2006). It would appear that the ecology of the individuals from each of the two laying episodes would be different. In *Palaemon macrodactylus*, which lives for about a year, the females from the different annual laying episodes also form cohorts with a different size and a staggered reproductive period the following year (Vázquez et al., 2012). This raises questions about the establishment success of juveniles from each laying season in *P. serratus* and about competition between individuals between cohorts.

Our results suggest that as females age, they breed earlier in the season. Earliness of reproduction with the length of the females has been observed in *P. macrodactylus* (Vázquez et al., 2012), *Palaemon pugio* (Alon and Stancyk, 1982) and *Palaemon varians* (Oliphant and Thatje, 2021). As winter laying gets earlier with the age of the *P. serratus* females, older females could allow the third annual laying mentioned by several authors (Cole, 1958; Campillo, 1979).

#### 4.2. Trade-off between egg biomass and fecundity

As expected, total clutch weight, which is limited by the volume of their incubation cavity, was strongly correlated with female length. Laying season appeared to have a significant influence on clutch weight, but this could be due to the heterogeneity of female length in each month (no interactive effect between season and female length on clutch weight; Table 2). Consistent with studies on *P. serratus* (Huxley, 2011; Emmerson et al., 2017), fecundity was correlated with female length. The smallest females sampled were 60 mm long and had a clutch of about 1100 eggs. Their size is close to the minimum size among known egg-bearing females of this species, i.e. 55 mm (Forster, 1951; Fahy et al., 2006). The 2 females over 100 mm sampled in summer had clutches of over 6000 eggs, while the 12 females of the same size sampled in winter had an average fecundity of 3759 eggs. Our results are consistent with those of other authors describing fecundity ranges in this species (550–7000, Sollaud, 1923; 1523–4282, Forster, 1951; 900–5000, Campillo, 1979; about 1500–6500, Huxley, 2011; 550–6100, Felício et al., 2002; 221–5121, Emmerson et al., 2017).

The relationship between the size of the females and the average biomass of their eggs varied seasonally. In winter and spring, older females produced larger eggs than younger females. In summer, however, the biomass per egg did not vary with the size of the females. In old females, we observed a seasonal decrease in biomass per egg (Fig. 3; on average 0.18 mg in winter, 0.15 mg in spring and 0.13 mg in summer for I+ females) accompanied by an increase in fecundity. The negative correlation between relative biomass per egg and relative fecundity suggests they produce relatively lower expensive offspring, but in greater quantities. This pattern is observed in decapods (Guzmán et al., 2016; Oliphant and Thatje, 2021) as well as in arthropods in general (Fox and Czesak, 2000). The trade-off between fecundity and egg biomass is determined by environmental conditions during oogenesis (i.e. several months before laying in *P. serratus*). Reduced daylength in autumn has been shown in other species to determine the production of large eggs during winter oviposition, whereas increased daylength in spring would lead to the production of small eggs during summer oviposition (Bouchon, 1991a, 1991b; Urzúa et al., 2012). The combination of temperature dynamics and day length could thus determine the trade-off between these reproductive traits (Little, 1968; Olive and Pillai, 1983; Wang et al., 2020).

#### 4.3. Fatty acid composition of eggs

Lipids are the main fuel used during embryonic development, accounting for 29 and 11 % of the dry weight of eggs at the start and end of embryonic development respectively in *P. serratus* (Narciso and Morais, 2001). All the eggs analysed here were rich in fatty acids (around 200 µg/mg dry weight), dominated by PUFAs, including EPA (around 20 % of total FAs). Crustacean larvae require LC-PUFAs for development, such as EPA (Anger, 1998; Bergé and Barnathan, 2005). PUFAs maintain membrane integrity and viscosity (Pagliarani et al., 1986; Estévez and Kanazawa, 1996; Los and Murata, 2004), especially in cold waters (Harwood, 1988; Munro and Thomas, 2004). Here, the total concentration of FA as well as EPA and DHA decreased throughout the laying season. As these FAs are particularly necessary in cold water, our results indicate a maternal effect, i.e. that females optimize their fitness from the start of their reproductive cycle (during ovarian development) in anticipation of the environmental conditions encountered by the embryos during their development several months later. This is even more true for older females, as the eggs are larger and more concentrated in FA.

Egg concentration in 18:2n-6 and 18:3n-3 increased sharply during the laying season (on average from 0.89 % in winter to 2.35 % in summer and 0.73 % in winter to 3.23 % in summer respectively). These FAs are known to be consumed during embryonic development in *P. serratus* (Narciso and Morais, 2001; Morais et al., 2002). This is an

intriguing result, since these are the only fatty acids for which the concentration increases, and they form the basis of the omega 6 and 3 synthesis pathways respectively. The ability to synthesize long-chain PUFAs is not well known in crustaceans, but biosynthesis from 18:3n-3 is possible in some shrimp larvae (Jones et al., 1979; Kanazawa et al., 1979b, a; Roustaian et al., 1999). As the capacity for FA biosynthesis increases with summer temperatures (Mika et al., 2014), females could store more LC-PUFA in summer, passing on less to their offspring.

The most common FAs were the same as those already described in the eggs of *P. serratus* and related species (Narciso and Morais, 2001; Morais et al., 2002). The relative composition of FA eggs did not vary with either the age of the females or the laying season. However, the diet of *P. serratus* females varies during their life cycle, in relation to their seasonal lateral migrations and/or their change in trophic status (Forster, 1951; Campillo, 1979; González-Ortegón et al., 2018). These results, and the seasonal variations in egg composition which remain lower than expected, are counter-intuitive. They imply that the reproductive allocation of females is controlled. Females allocate part of the FAs assimilated from their food to reproduction, but also part that is stored or used for growth. It is possible that the fraction of FAs allocated to the ovaries is more constant in terms of composition than that allocated to the hepatopancreas, an observation made between winter and summer *Pleuroncodes monodon* females (Bascur et al., 2018). 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).

#### 4.4. Maternal effects become increasingly appropriate with age

The results presented here are an interesting illustration of maternal effects. As they grew older, the females produced larger eggs in winter but not in summer, in keeping with the harshness of the environment. As well as receiving more biomass, which is known to increase the performance of offspring in decapods (Hancock, 1998; Giménez et al., 2004; Torres et al., 2020), the eggs were more concentrated in FA and in particular in DHA and EPA, essential PUFAs all the more necessary in cold water (Harwood, 1988; Munro and Thomas, 2004). Eggs that have received the highest amount of FA will probably produce larvae with more FA at hatching, giving them a better chance of survival in difficult environmental conditions (Palacios et al., 2001; Holme et al., 2009). This could explain why females lay their eggs earlier and earlier as they get older. Positive relationships between the lipid content of eggs and larval nutritional vulnerability have been described for other crustacean species in temperate regions (Andrés et al., 2010; Urzúa et al., 2012; Rotllant et al., 2014).

However, there is no guarantee that the extra energy transmitted to the winter eggs will be inherited when the larvae hatch. Indeed, the low temperatures experienced during the incubation of the winter eggs lead to increased consumption of embryonic lipid reserves. (Wehrtmann and López, 2003; Brillon et al., 2005; Baudet et al., 2023). The over-consumption of embryonic lipid reserves in winter could erase the initial advantage of winter embryos which could explain the contradictory results on the relationship between the age of *P. serratus* females and the reserves available when the larvae hatch, followed by their performance (González-Ortegón et al., 2013, 2015, 2018; Baudet et al., 2022).

## 5. Conclusion

The reproductive season for *P. serratus* runs from December to July, during which females lay eggs twice from their second year of life and increasingly earlier as they get older. Females increase their investment in reproduction as they age and older females make a seasonal compromise by maximising eggs quality in winter and eggs quantity in summer. In addition, winter eggs are more concentrated in FA and in



particular in the essential PUFA needed in cold water. These results raise questions about the mechanisms underlying these maternal effects.

### CRedit authorship contribution statement

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

### Declaration of competing interest

The authors have no competing interests to declare that are relevant to the content of this article.

### Data availability

Data will be made available on request.

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### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jembe.2024.152056>.

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