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Jason Jeanne, Jean-Baptiste Baudet, Benoît Xuereb, Aurélie Duflot, Agnès Poret, et al.. Influence of salinity on the larval development and juvenile fitness of the estuarine shrimp *Palaemon longirostris*. *Journal of Experimental Marine Biology and Ecology*, 2026, 597, pp.152180. <10.1016/j.jembe.2026.152180>. <hal-05559568>

**HAL Id: hal-05559568**

**<https://normandie-univ.hal.science/hal-05559568v1>**

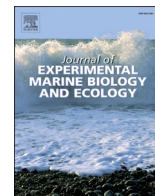
Submitted on 20 Mar 2026

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## Influence of salinity on the larval development and juvenile fitness of the estuarine shrimp *Palaemon longirostris*

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### ARTICLE INFO

#### Keywords:

Larval development  
*Palaemon longirostris*  
Phenotypic plasticity  
Salinity  
Estuarine ecology

### ABSTRACT

Salinity fronts structure the nursery habitat of the estuarine shrimp *Palaemon longirostris*. This species inhabits estuaries in Western Europe and North Africa. Using a salinity gradient representative of estuarine conditions (10, 15, 20, 25, and 30 PSU), we evaluated the effects of salinity on larval history traits (including larval survival, developmental pathways, duration of larval development, metamorphosis success, larval weight gain and juvenile weight). Our results demonstrate that increasing salinity towards marine levels shortened larval development time and improved metamorphosis success, with the best results observed at 25 PSU. Juvenile weight and weight gain were significantly higher at elevated salinities, indicating a positive relationship between salinity and larval fitness. Conversely, low salinities were associated with reduced survival and performance, indicating limited osmoregulatory capacity in response to osmotic stress. These findings emphasize the important role of salinity in determining the phenotypic plasticity and survival of *P. longirostris* larvae. Together, these results highlight an operational optimum of around 25 PSU in the laboratory and sharp declines in performance at the extremes of the estuarine gradient. By clearly demonstrating for the first time an optimum high salinity level for the larval development of *P. longirostris*, this study provides original insights into the life cycle and population dynamics of this species.

### 1. Introduction

For marine crustaceans, colonising brackish nurseries provides substantial nutritional opportunities (Barbier et al., 2011). However, osmoregulation (i.e. the active control of internal osmotic pressure) is costly in terms of energy. Therefore, colonising such habitats can represent a significant ecological opportunity for marine crustaceans. This transition to estuaries has occurred independently in several taxonomic groups (Anger, 2013; Wolfe et al., 2023). Many euryhaline adult species can thrive under such conditions thanks to their well-developed regulatory machinery. However, the capacity and tolerance windows of eggs and larvae are often limited (Charmantier, 1998; Anger, 2001; Ituarte et al., 2016). Salinity is widely recognised as a key environmental factor shaping larval development in decapods. The development of osmoregulatory function is also a critical factor influencing survival, particularly in euryhaline species (Anger, 1985; Charmantier, 1998; Anger, 2003; Torres et al., 2002; Torres et al., 2011; Torres et al., 2021a, 2021b). Osmoregulatory systems in the early larval stages are often

immature or underdeveloped, making these stages susceptible to osmotic stress (Ituarte et al., 2016). However, some species, such as *Macrobrachium petersi*, exhibit osmoregulatory capabilities from hatching onwards (Read, 1984; Charmantier, 1998). This ontogenetic constraint provides a mechanistic basis for the broad range of salinity-driven effects documented in decapod larvae, including growth, feeding rates, morphological development, the duration and number of larval stages, and physiological traits such as dry weight and lipid/protein content (Anger, 1985; Gonçalves et al., 1995; Torres et al., 2002; Torres et al., 2002; Anger, 2003; Ituarte et al., 2016; Torres et al., 2021a, 2021b; Xu and Zeng, 2023).

Various adaptive strategies have evolved among decapod species to cope with physiological constraints and mitigate the risks associated with salinity fluctuations during the early stages of development. In some taxa, the developmental process is abbreviated, with one or more of the early zoeal stages being completed within the egg envelope during embryogenesis. The resulting larvae then emerge as advanced zoea, megalopae or even juveniles, which minimises osmotic stress

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(Charmantier, 1998). However, due to their small size and limited swimming ability, decapod larvae are generally unable to avoid such fluctuations. For estuarine species, a common alternative strategy is larval export. Larvae are carried seaward by the tide and residual estuarine circulation into saltier marine waters, where they complete their development. This phenomenon has been well documented in mangrove crabs (Britto et al., 2018) and shrimp species (Oliphant and Thatje, 2014) inhabiting semi-isolated coastal water bodies. In some species, however, female behavioural adaptations complement larval strategies. Ovigerous females may migrate towards saltier zones of the estuary to lay eggs or release larvae, thereby increasing their chances of survival in the early stages of life. This behaviour has been observed in several crab species, including *Callinectes sapidus* and *Scylla serrata* (Tankersley et al., 2002; Nurdiani and Zeng, 2007). Beyond these movement-based strategies, ontogenetic changes in osmoregulatory capacity are also important. Several studies have demonstrated that osmoregulatory function varies across larval stages, often aligning with ecological strategies (Charmantier et al., 2002; Cieluch et al., 2004; Torres et al., 2011; Ituarte et al., 2016). For example, the initial zoeal stage of *Neohelice granulata* exhibits robust hyperosmoregulatory capacity, which facilitates survival in estuarine environments. Conversely, later stages that develop offshore demonstrate reduced osmoregulatory function, regaining it just before reintegration into estuarine habitats (Charmantier et al., 2002). Together, these adaptations emphasize the significant selective pressures imposed by salinity variability on early developmental stages, as well as the intricate evolutionary responses that have emerged to address these challenges.

In addition to physiological adaptations, developmental plasticity enables larvae to adjust their growth and development in response to environmental variability. The early life stages of decapods are characterised by a high degree of developmental plasticity, meaning the ability of a single genotype to produce multiple phenotypes. This allows them to adapt to the dynamic and frequently unpredictable conditions of their habitats (West-Eberhard, 2003). Two outcomes are especially relevant here: (i) abbreviated development (fewer developmental stages under favourable conditions), and (ii) supernumerary stages (i.e. the insertion or repetition of larval instars yielding intermediate morphologies without a new stage identity) (Anger, 2001; West-Eberhard, 2003; Oliphant et al., 2013; Baudet et al., 2022; Baudet et al., 2024). These shifts in developmental pathways alter the timing of metamorphosis and total larval duration, thereby modulating exposure to estuarine variability (Pechenik, 1990; Forward et al., 2001; Oliphant et al., 2013; Baudet et al., 2024). However, these adjustments incur costs: added or repeated instars prolong development, delaying settlement and slowing growth. They also often result in smaller, more depleted juveniles with lower lipid reserves and higher mass-specific respiration (Anger, 2001; Oliphant et al., 2013; Baudet et al., 2024).

*P. longirostris* is an estuarine species of shrimp belonging to the genus *Palaemon*, found along the coasts of Western Europe and North Africa. It is targeted by small-scale fisheries in several Western European estuaries. Its average lifespan is estimated to be around two years (Béguet et al., 2010; de Carvalho-Souza et al., 2025). Reproductive activity in this species is seasonal, typically occurring once per year, with a spawning peak in May (Sorbe, 1983; de Carvalho-Souza et al., 2025). Benthic adults can be found far upstream, where salinity can drop to near zero at low tide (Cartaxana, 1994). Females carry their eggs attached to their pleopods and release the larvae into the water column upon hatching, where they undergo a series of zoeal stages (Gurney, 1924; Sorbe, 1983; Fincham and Figueras, 1986). In laboratory, larval development typically lasts about twenty days, though this can vary with temperature, as observed in other Palaemonid shrimp species. Despite the recognised importance of salinity for decapod larvae, there is almost no empirical data on *P. longirostris*, and the optimal salinity for its larval development remains largely unknown. To address this issue, we established a baseline performance curve by isolating salinity and determining the optimal conditions for larval development. To date, no

study has systematically examined how larval performance of *P. longirostris* varies along an estuarine salinity gradient, leaving three questions unanswered: i) where along the estuarine gradient does performance peak; ii) what are the lower-upper tolerance bounds; iii) and how do multiple traits (survival, developmental pathway/duration, metamorphosis success, and juvenile carryover weight) co-vary? Here, we address these questions by mapping the full larval response across a controlled salinity gradient. This integrated, multi-endpoint design moves beyond binary “brackish vs marine” comparisons to provide operational laboratory thresholds. Our study shifts the narrative from whether salinity matters to where and by how much it matters for *P. longirostris* larvae.

## 2. Materials and methods

### 2.1. Collection and maintenance of egg-bearing females

On 17 May 2023, egg-bearing females were collected from the Seine-Maritime in France (49°28'29" N, 0°27'42" E) below the Tancarville Bridge using fishing nets dragged along the riverbed. To standardise embryogenesis and minimise variability in larval performance between females, they were collected at the start of the breeding season and reared in the laboratory until hatching. They were then transported to the laboratory in buckets filled with oxygenated site water. They were kept in their native estuarine water (7.6 PSU and 15.9 °C, as measured by a refractometer, Hannah Instruments), with gradual increases to 15 PSU and 18 °C (at a rate of 1 PSU and 1 °C per hour). Three females of a similar size with advanced-stage embryos were selected. The females had a mean ( $\pm$  S.D.) total length of 55.6  $\pm$  3.8 mm and a mean length of cephalothorax of 15.3  $\pm$  0.6 mm, respectively (from the base of eye-stalks to the posterior edge of cephalothorax). These females represent an older part of the population, particularly when compared to published values for ovigerous females, which typically range from 7.1 to 14.6 mm with an average cephalothorax length of 9.8  $\pm$  1.4 mm in the Gironde Estuary (Béguet et al., 2010). Furthermore, due to their larger size, these ovigerous females can carry an average of 547 eggs, ranging from 78 to 1391 (Béguet et al., 2010). This elevated fecundity is indicative of older, larger females, which produce more eggs per brood. By selecting such individuals, we aimed to maximise larval production and ensure a robust and consistent supply for our experimental conditions. After the acclimatisation phase, the females were kept for 19  $\pm$  1 days until hatching. They were isolated in insulated baskets immersed in a 100 L temperature-controlled tank at 17.9  $\pm$  0.14 °C (regulated at  $\pm$ 0.1 °C by a TECO TK700 cooling unit), with water constantly circulating in closed system at 15 PSU by means of a pump. The water was supplied by a mixture of UV-treated, filtered seawater from Deauville (Normandy, France) and dechlorinated tap water, which was mixed using a stirring pump. The water level was monitored daily and topped up as necessary. The plastic baskets have small holes to allow water and larvae to circulate when they hatch. The baskets were supported by a base covered with a thin layer to collect the larvae once hatched. The photoperiod was a 12-h light/dark cycle, and the females were fed three times a week with squid pieces. The following parameters were measured once a week for each tank: dissolved oxygen (oximeter, Oxyguard); salinity (refractometer, Hanna Instruments); pH (pH meter, Oxyguard); and ammonium concentration (Visocolor NH<sub>4</sub><sup>+</sup> and PF12plus spectrophotometer, Hanna Instruments). One-third of the seawater was replaced weekly to avoid ammonium accumulation (less than 1 mg/L; Kur and Öz, 2015).

### 2.2. Exposure of larvae to a salinity gradient

The experimental protocol was adapted from the larval monitoring method developed by Baudet et al. (2022) for *P. serratus*. On the day of hatching, while the larvae were in the zoea 1 stage, they were isolated from the females and collected using phototaxis. Three groups of 50

active larvae per female were collected at hatching using a pipette. The larvae were then rinsed with distilled water and weighed. To assess the effect of salinity, five groups of 50 live larvae per female were isolated. Each group was placed in an aerated 500 mL conical container filled with filtered, UV-treated seawater that had been adjusted to different salinities (10, 15, 20, 25 and 30 PSU) by adding dechlorinated tap water. To prevent mixing of larval stages and predation, larvae from different broods were not pooled under the same conditions. This approach enabled us to evaluate potential maternal influences on larval development. Females were subsequently studied as a random factor in the analyses. The conical vessels were placed in a single water bath at a constant temperature of 18 °C (regulated to within ± 0.1 °C by a TECO TK700 cooling unit) and maintained on a 12-h light/dark cycle. The water was completely renewed three times a week. The chosen temperature of 18 °C is the same as that measured at the bottom of the estuary near Tancarville, where the larvae are released between May and July (GIP Seine-Aval). The experiment extends from hatching to metamorphosis into juveniles. The larvae were fed *ad libitum* daily with freshly hatched *Artemia spp. nauplii* at a concentration of 10 per mL, as recommended for maintaining a close species throughout all larval stages (*P. serratus*: Reeve, 1969; Campillo, 1979; Baudet et al., 2024). On days without water changes (four days per week), half the usual amount of *Artemia* was added to each conical vessel to prevent ammonium accumulation (always *ad libitum*). Once a week, prior to the water change, the same physicochemical parameters as those monitored during female maintenance were measured, except for salinity, which was measured twice weekly (Table 1). Observed salinities were close to the nominal values. On average, oxygen saturation was 95.94 ± 3.01 %, pH was 7.91 ± 0.07 % and ammonium was at 0.75 ± 0.09 mg/L (levels below 1 mg/L as recommended by Kir and Öz, 2015). During water renewal, live larvae were counted. At the same time, their larval stage was monitored. Larval stage description was based on morphological criteria observed and derived from Fincham and Figueras (1986) and Gurney (1924), as described in Table 2. Although the larvae were reared in groups, the observed distribution of larval stages was interpreted as representative of progression through successive stages. After metamorphosis, the juveniles were patted dry using absorbent paper and weighed. Based on the average weight of the larval group at hatching and the individual weight of the juveniles, weight gain was calculated as a function of days (the mass of the juveniles was subtracted from the estimated mass of the larvae, and the result was divided by the number of days) from hatching to metamorphosis.

### 2.3. Statistical analysis

Statistical analyses were performed using R 4.3.3 software (R Core Team, 2022). Brood identity (*i.e.* female) was included *a priori* as a random intercept in all mixed models, to account for the non-independence (*i.e.* clustering) of larvae from the same female, as well as for potential maternal heterogeneity. The effects of salinity on

**Table 1**  
Average physico-chemical conditions (± S.D.) in the tank monitored during the larval phase of *Palaemon longirostris*.

Temperature (°C)	Salinity (PSU)	Dissolved oxygen (%)	pH	Ammonium (mg. L <sup>-1</sup> )
17.97 ± 0.06	10.5 ± 0.34	95.1 ± 3.20	7.96 ± 0.17	0.75 ± 0.50
	15.2 ± 0.44	99.7 ± 5.07	7.93 ± 0.16	0.66 ± 0.28
	20.1 ± 0.48	91.4 ± 1.68	7.79 ± 0.14	0.66 ± 0.28
	24.9 ± 0.60	96.5 ± 3.46	7.97 ± 0.05	0.87 ± 0.47
	30.0 ± 0.74	96.8 ± 1.06	7.93 ± 0.06	0.83 ± 0.57

Values represent the mean ± SD

**Table 2**  
Morphological criteria selected for the identification of the larval stages of *Palaemon longirostris*. Only new criteria appearing for each stage during development are annotated in the table.

Stages	Morphological criteria			
	(Fincham and Figueras, 1986)	(Gurney, 1924)	Present study	
Zoea	1	1	1	Sessile eyes Rostrum without dorsal spine
	2	2	2	Pedunculated eyes 1 rostral spine Pleopod buds
	3	3	3	2 rostral spines Pleopod buds 3 rostral spines
	4		4	Pleopod rudimentary Pleopod rudimentary
	5	5	5	Pleopod with rudimentary setae
	6		6	Endopod of pleopods with well-developed appendix interna
	7			Rostrum with >6 dorsal teeth
Juvenile				

larval development time, metamorphosis rate, juvenile weight and weight gain were analysed using linear mixed-effects models (Fig. 1). We checked the normality and homoscedasticity of the residuals for these metrics using Q-Q plots, residuals vs fitted plots and Levene's test on the residuals by salinity. A log-transformed LMM produced similar results for salinity. Development time and metamorphosis success were analysed using GLMMs (glmer function, lme4 package), with salinity as a fixed effect and female identity as a random effect. Development time was modelled with a Poisson error distribution (log link), while metamorphosis success used a binomial error distribution. For the Poisson GLMM (development time), residual diagnostics with DHARMA indicated significant underdispersion (uniformity test, *p*-value < 0.001; dispersion statistic = 0.17). We assessed dispersion using Pearson's chi-squared test and found no evidence of overdispersion (Pearson's chi-squared test / residual degrees of freedom = 0.166, *p*-value = 1.00). For the binomial GLMM (metamorphosis success), we examined the residuals using DHARMA. The tests indicated adequate calibration (KS: D = 0.228, *p*-value = 0.361), no overdispersion (dispersion = 1.59, *p*-value = 0.14), and no zero inflation (*p*-value = 1). Pairwise comparisons were performed using the glht function (multcomp package) with Tukey's adjustment. Juvenile weight and biomass gain were analysed using LMMs (lmer function, lme4 package) with salinity as the fixed effect and female identity as the random effect. Predicted marginal means were computed using the emmeans function (emmeans package) and *post hoc* comparisons were performed using Tukey's adjustment (pairs function, emmeans package). A significance threshold of α = 0.05 was used for all analyses. *Post hoc* pairwise comparisons were performed among salinity levels using the multcomp::glht function with Tukey's all-pairs contrasts. *P*-values and confidence intervals were adjusted using the "single-step" procedure, which provides strong family-wise error rate (FWER) control across all pairwise contrasts. To assess the importance of each variable in explaining the variability of the data, we used two R<sup>2</sup> indicators: marginal R<sup>2</sup> and conditional R<sup>2</sup> (package performance and MuMIn for metamorphosis success). Marginal R<sup>2</sup> measures the proportion of variability explained by the model's fixed variables (*e.g.* salinity), while conditional R<sup>2</sup> quantifies the variability explained by all fixed and random effects (*e.g.* the random effect of female). For each model, the explanatory share of the random female effect was obtained by calculating the difference between the conditional R<sup>2</sup> and the marginal R<sup>2</sup> (Nakagawa and Schielzeth, 2013; Nakagawa et al., 2017).

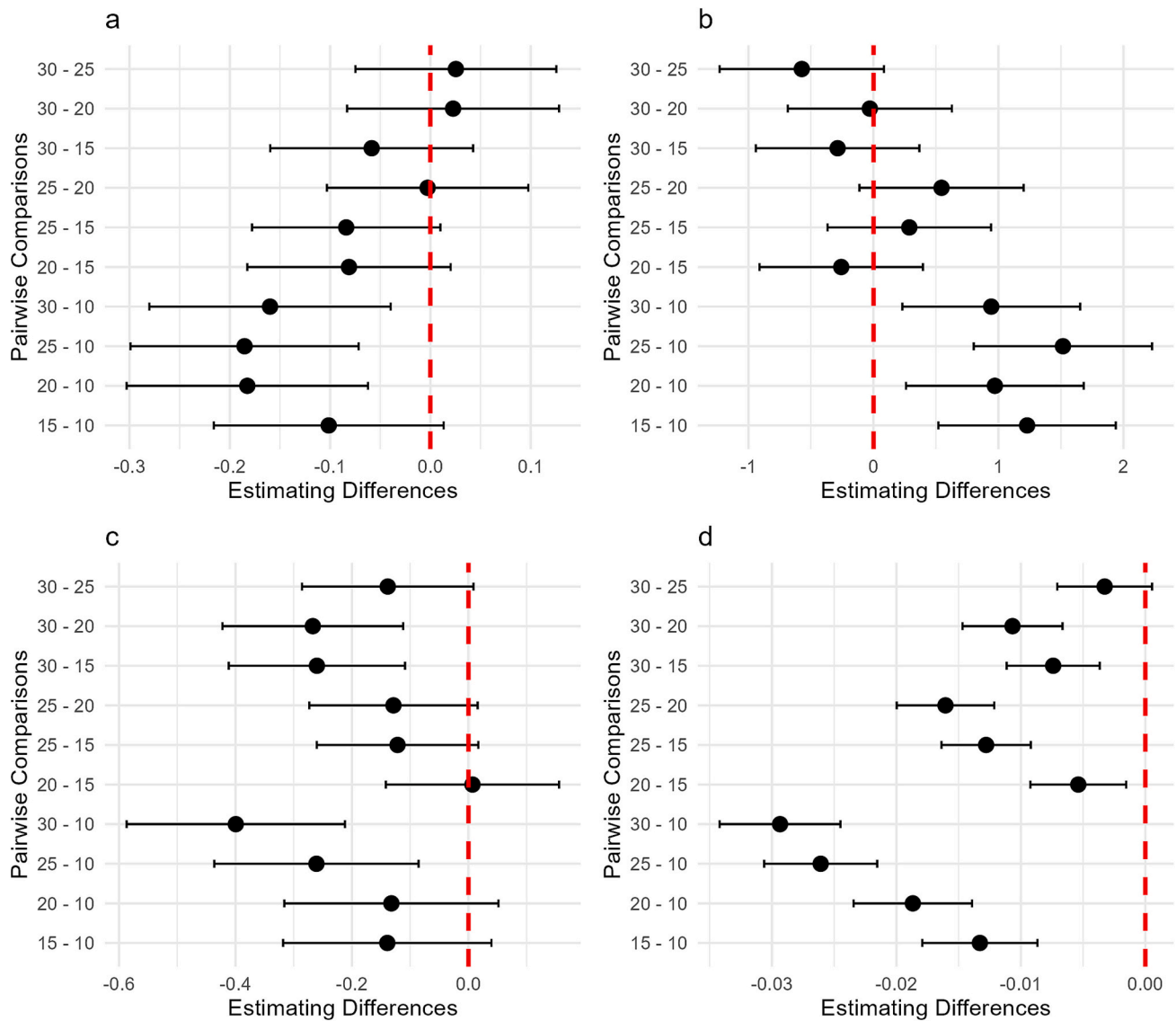


Fig. 1. Pairwise comparisons of the response of *Palaemon longirostris* larvae in function of salinities. A: larval development time. B: metamorphosis rate. C: weight at metamorphosis. D: weight gain per day of larval development. Salinities are given in PSU.

### 3. Results

#### 3.1. Quality from laying at hatching and development pathway

Upon hatching, the larvae had a homogeneous wet weight, with an average weight ( $\pm$  S.D.) of  $0.25 \pm 0.01$ ,  $0.23 \pm 0.01$  and  $0.26 \pm 0.01$  mg per larva for females 1, 2 and 3, respectively. Six larval stages were observed during development (Fig. 2). However, seven larval stages were observed for the larvae of female 2 at a salinity of 10 PSU. This additional stage, which was not observed in the other females during the experiment (nine larvae out of fifty were observed), was named stage 2'. This new stage had not previously been documented in the two main classification systems for the larval stages of this species (Fincham and Figueras, 1986; Gurney, 1924). This early developmental stage is characterised by stalked eyes, a rostral spine, and most notably, pleopod buds, which distinguish it from stage 2.

#### 3.2. Larval and juvenile survival

Fig. 3 shows that survival declined over time at all salinities, with significantly higher early mortality at 10 PSU, moderate declines at 15

PSU and relatively stable survival at 20, 25 and 30 PSU. For juveniles, the results showed a general trend towards an increase in the metamorphosis rate with increasing salinity (Fig. 4). A generalized linear mixed effects model demonstrated significant effects (10–15:  $p$ -value  $\leq 0.001$ ; 10–20:  $p$ -value = 0.001; 10–25:  $p$ -value  $\leq 0.001$ ; 10–30:  $p$ -value = 0.002), with the lowest salinity of 10 PSU showing the greatest difference from all other salinities (Fig. 1). The lowest rates were observed at 10 PSU, with a mean value ( $\pm$  S.D.) of 23.3% ( $\pm 14.04$ ) for all females (Table 3). An increase in the metamorphosis rate was noted from 15 to 25 PSU, with respective values of 49.3% ( $\pm 17.47$ ), 43.3% ( $\pm 25.0$ ) and 56.0% ( $\pm 19.69$ ). At 30 PSU, the metamorphosis rate decreased slightly compared to 25 PSU, reaching 42.6% ( $\pm 24.11$ ). Inter-female heterogeneity was non-negligible. The random female intercept had a variance of  $\sigma^2$  (female) = 0.280 (SD = 0.530, logit scale), corresponding to an intraclass correlation of  $ICC \approx 0.079$  (i.e.  $\sim 7.9\%$  of residual heterogeneity is attributable to female identity after accounting for salinity). This aligns with  $R^2$  marginal = 0.446 (salinity only) versus  $R^2$  conditional = 0.895 (salinity + female). Female identity accounted for  $\sim 45\%$  of the total variance (conditional  $R^2$  – marginal  $R^2$ ).

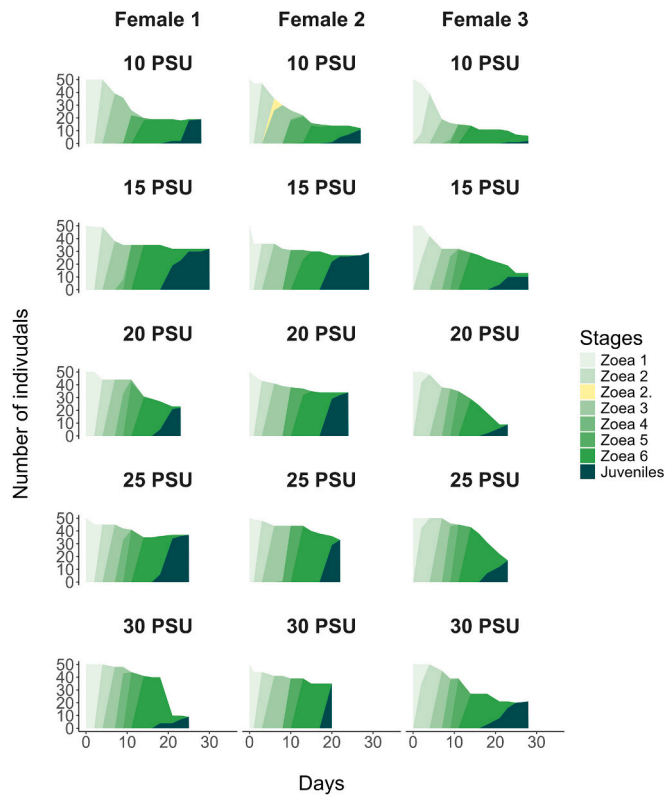


Fig. 2. Tracking the development of batches of 50 *Palaemon longirostris* larvae incubated at 18 °C at 10, 15, 20, 25 and 30 PSU. Salinity values are given in PSU.

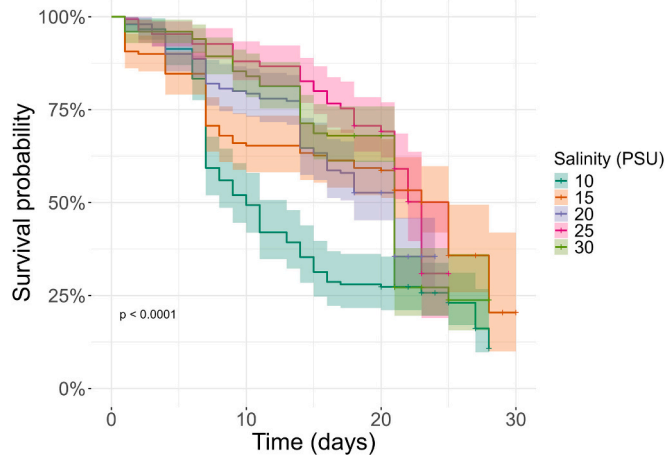


Fig. 3. Survival probability curve for *Palaemon longirostris* larvae exposed to different salinity concentrations from hatching to metamorphosis ( $n = 150$  larvae per salinity; total  $N = 750$ ). Salinity values are given in PSU.

### 3.3. Larval development time

Significant differences in development time to metamorphosis were observed at salinities of 10–20, 10–25 and 10–30 PSU (Fig. 1). In fact, at lower salinities (10 and 15 PSU), it took longer to complete metamorphose (Table 3). At 10–15 PSU, metamorphose and development took longer. At 20–30 PSU, development was shorter and stabilised around ~20 PSU (Fig. 5). Differences were also observed among females. Larvae from female 2 exhibited the shortest development times across most salinities, with an average ( $\pm$  S.D.) development time of

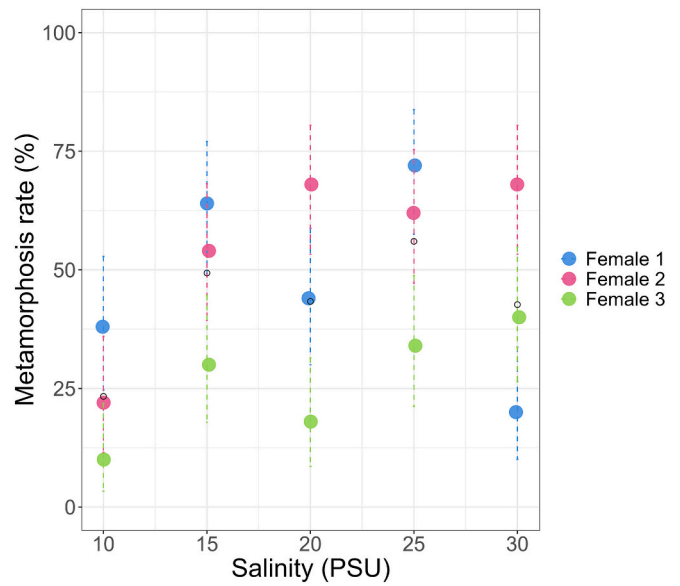


Fig. 4. Rate of metamorphosis (%) of *Palaemon longirostris* larvae exposed to a salinity gradient throughout their larval development, from hatching to metamorphosis. Light circles represent averages.

Table 3

Averages developmental parameters and fitness-related traits of *Palaemon longirostris* larvae at different salinity levels.

Endpoint	10 PSU	15 PSU	20 PSU	25 PSU	30 PSU
Development time (days)	24.65 $\pm$ 2.01	22.27 $\pm$ 2.54	20.49 $\pm$ 1.32	20.47 $\pm$ 1.42	20.98 $\pm$ 2.13
Metamorphosis rate (%)	23.33 $\pm$ 14.04	49.33 $\pm$ 17.47	43.33 $\pm$ 25.01	56.00 $\pm$ 19.69	42.66 $\pm$ 24.11
Weight of juvenile (mg)	1.85 $\pm$ 0.30	1.99 $\pm$ 0.28	1.95 $\pm$ 0.33	2.11 $\pm$ 0.28	2.23 $\pm$ 0.47
Weight gain (mg/day)	0.06 $\pm$ 0.01	0.07 $\pm$ 0.01	0.08 $\pm$ 0.01	0.09 $\pm$ 0.01	0.09 $\pm$ 0.01

Values represent the mean  $\pm$  SD; PSU: Practical Salinity Unit

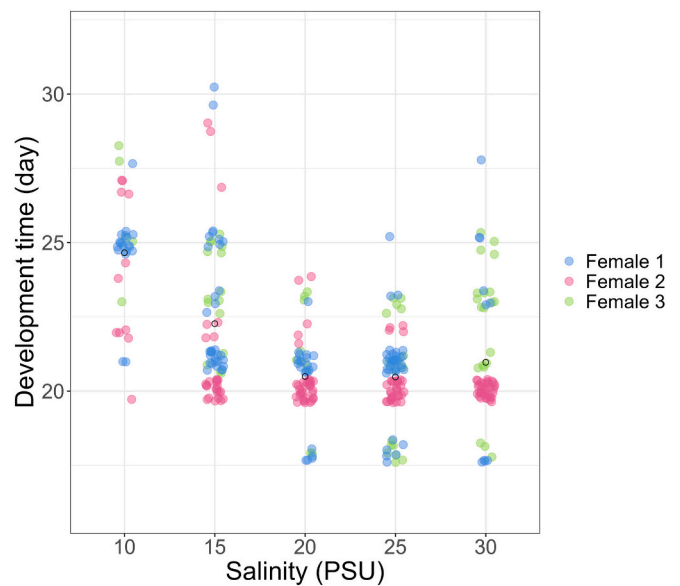


Fig. 5. Developmental time to metamorphosis of *Palaemon longirostris* larvae exposed to a salinity gradient. At hatching, the larvae were grouped in triplicate batches of 50. Light circles represent averages. Each dot represents a juvenile.

20.72 ± 1.84 days, compared to 21.93 ± 2.52 and 22.06 ± 2.52 days for females 1 and 3, respectively, regardless of salinity (Table 3). This difference was clearly observed at salinities of 20, 25 and 30 PSU, with average durations of 20.41 ± 1.08, 20.25 ± 0.68 and 20.00 ± 0.00 days, compared to 20.40 ± 1.40, 20.72 ± 1.47 and 21.90 ± 3.66 days for female 1, and 21.00 ± 1.94, 20.35 ± 2.18 and 22.15 ± 2.25 days for female 3. Variance in development time at the female level was negligible. The random intercept standard deviation (SD) was 0.012 on the log scale (± 1.2% multiplicative shift in expected duration between females). The model's  $R^2$  marginal = 0.071 and  $R^2$  conditional = 0.074 ( $\Delta R^2 = 0.003$ ) suggest that salinity rather than female identity captures most of the variation (0.3%). We therefore retain the random intercept *a priori* to account for within-female clustering, but do not assign it a biological interpretation.

### 3.4. Juvenile fitness

Finally, the wet weight of juveniles is obtained at metamorphosis (Fig. 6). Using a linear mixed effects model, significant effects were found for salinities of 10–25 ( $p$ -value = 0.0005), 10–30 ( $p$ -value < 0.0001), 15–30 ( $p$ -value < 0.0001) and 20–30 ( $p$ -value < 0.0001) (Table 3; Fig. 1). Juvenile weight (± S.D.) increased from 1.85 ± 0.30 mg at 10 PSU to 2.23 ± 0.47 mg at 30 PSU (Table 3). Adding the female random effect to the linear mixed model considerably improves the model's fit. Salinity-related fixed effects explain around 10.5% of the variability in juvenile weight; accounting for inter-female differences, however, explains 29.3%. The female effect alone explains around 18.8% of the total variance. Daily weight gain increased with salinity (global test,  $p < 0.001$ ; Fig. 7). The average values (mg day<sup>-1</sup> ± S.D.) were 0.065 ± 0.009 at 10 PSU, 0.078 ± 0.009 at 15 PSU, 0.082 ± 0.010 at 20 PSU and 0.091 ± 0.010 at 25 PSU (Table 3). Values at 30 PSU remained high and could not be distinguished from those at 25 PSU (Fig. 1). Thus, juveniles at 25 PSU grew approximately 40% faster than those at 10 PSU. Adding a random female intercept had a modest effect on the fit, with marginal  $R^2 = 0.355$  (salinity only) and conditional  $R^2 = 0.424$  (salinity + female), that is,  $\Delta R^2 = 0.069$  (6.9%).

## 4. Discussion

This study evaluates the response of *P. longirostris* larvae exposed to a

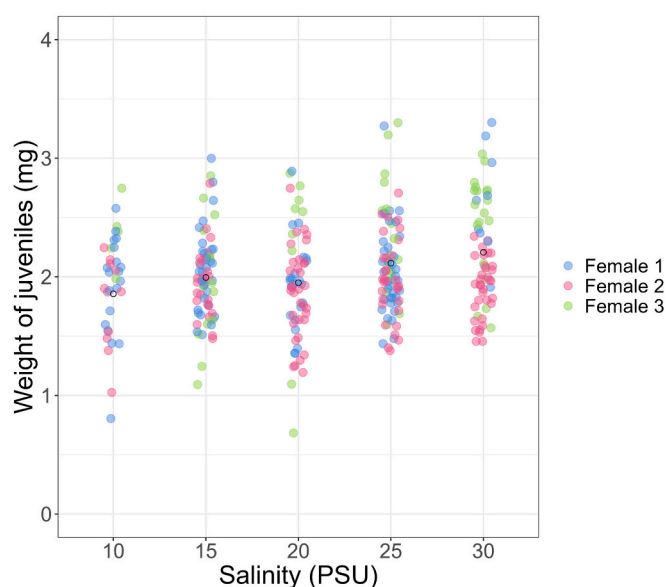


Fig. 6. Metamorphosis weight (mg) of *Palaemon longirostris* juveniles exposed to a salinity gradient throughout their larval development, from hatching to metamorphosis. Light circles represent averages.

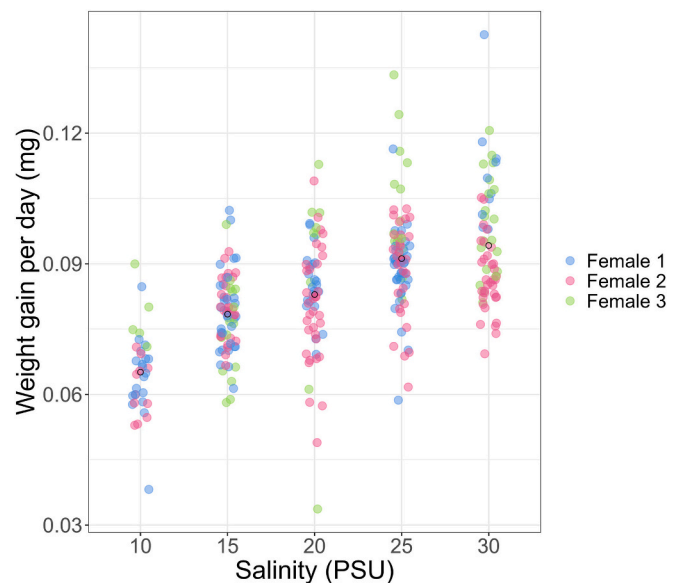


Fig. 7. Daily weight gain of *Palaemon longirostris* from hatching to juvenile metamorphosis of larvae exposed to a salinity gradient throughout their larval development. Light circles represent averages.

salinity gradient from hatching to metamorphosis. Several developmental metrics were assessed to understand the impact of salinity on larval performance. The data revealed that low salinity negatively affected survival, developmental pattern, duration, metamorphosis success, juvenile weight at metamorphosis, and daily weight gain. Larval development was clearly more successful at 30 PSU than at 10 PSU, confirming that *P. longirostris* requires export larvae to marine environments with higher salinity for optimal development.

### 4.1. Larval development patterns and phenotypic plasticity

Of the few studies that have focused on *P. longirostris* larvae, the main field keys used by the authors to determine the larval stage are those of Fincham and Figueras (1986; 1979), who describe seven larval stages, Gurney (1924), who describes five larval stages and Paula (1998), who also uses five larval stages. The variability in the number and morphology of larval stages in decapod species is well documented and has been attributed to phenotypic plasticity (Knowlton, 1974; Anger, 2001; Oliphant et al., 2013; Baudet et al., 2022; Baudet et al., 2024). In our experimental design, six larval stages were observed from hatching to metamorphosis across all salinity conditions tested. Larval developmental plasticity is well documented in decapods, whereby larvae adjust their developmental trajectories in response to physicochemical conditions (Criales and Anger, 1986; Oliphant et al., 2013; Baudet et al., 2024). This variability often reflects alternative developmental pathways, such as accelerated development involving fewer stages or prolonged development involving additional stages (Anger, 2001; Oliphant et al., 2013; Baudet et al., 2024). For instance, suboptimal salinity or nutrition can prompt prolonged development involving extra or repeated instars (Criales and Anger, 1986; Oliphant et al., 2013; Gonzalez-Ortegon and Gimenez, 2014). There is species-specific evidence for *P. longirostris*. Paula (1998) reported an additional fifth instar under 15 °C conditions, compared to four instars under warmer laboratory and field conditions. In our study, the occurrence of a seventh larval instar at 10 PSU (Female 2) is consistent with stress-induced developmental plasticity. Under hypo-osmotic conditions, the insertion or repetition of an instar occurs when larvae fail to reach the required size or condition for metamorphosis. These additional stages typically extend larval duration and delay metamorphosis, representing a common trade-off in situations of growth limitation or osmotic stress. This pattern was rare,

observed in only nine larvae, and absent at  $\geq 15$  PSU, which supports the idea of a salinity-linked mechanism rather than random variation. However, we acknowledge that maternal effects hypothesis or idiosyncratic variation cannot be ruled out.

González-Ortegón et al. (2016) studied larval development from hatching to metamorphosis under similar physicochemical conditions (i.e. individual monitoring of larvae in 50 ml per larva and feeding *ad libitum* at a rate of 10 *Artemia* sp. nauplii per ml) and reported an average development time of 24 days at 18 °C and salinities of 20 and 32 PSU. In our study, larvae exhibited a decrease in development time with increasing salinity. The average development time was longer at salinities of 10 and 15 PSU (24.6 and 22.3 days, respectively) than at salinities of 20, 25, and 30 PSU (20.5, 20.5, and 20.9 days, respectively) at 18 °C. Interestingly, the additional stage observed in the larvae of female 2 at 10 PSU did not appear to extend the development time. Once again, these differences can be explained by the plasticity of larval development. Although the physico-chemical rearing parameters were identical at 20 PSU and 18 °C, variations of around three days in total development time can be attributed to differences in larval rearing methods, such as individual versus group rearing (González-Ortegón et al., 2016). For example, Reeve (1969a) observed longer development times when rearing *P. serratus* larvae (a closely related species) individually rather than in groups. Another possible explanation is that differences in maternal provisioning and/or population of origin (Seine versus Porthmadog estuary in Wales) contribute to the observed differences (Holm, 1990). However, as genetic and physiological assays were lacking for these cohorts, this explanation remains speculative and would require common-garden rearing and genotyping to verify.

#### 4.2. Larval survival and metamorphosis success

The effects of salinity on larval survival are particularly pronounced at low levels of salinity. As shown in Fig. 3, survival probability declines progressively with increasing exposure duration, indicating a cumulative effect of salinity stress throughout larval development. Larvae exposed to 10 PSU experienced significant early mortality, as evidenced by a sharp decline in the survival curve. At 15 PSU, survival was also reduced, but the decline was more gradual. This suggests either partial acclimatisation capacity or less severe osmotic stress. By contrast, the convergence of the survival curves at 20, 25 and 30 PSU suggests lower, more stable mortality rates, likely due to less physiological compensation at these intermediate salinity levels. As zoea 1 larvae lack functional gills and instead rely on ion-transporting cells in the pleurae, inner branchiostegite epithelium and antennal glands for osmoregulation, with gill-based regulation only developing by zoea 4, we hypothesise that the mortality spike at 10 PSU reflects their limited capacity for early hypo-osmoregulation (Ituarte et al., 2016; Boudour-Boucheker et al., 2013). The timing of peak losses around day 8, during the transition from zoea 2 to 3, further suggests that the osmotic and energetic demands of molting exceed the transport capacity of the earlier stages. It is notable that the pace and robustness of this ontogeny varies across *Palaemonidae*, with species and populations differing in their early osmoregulatory competence (Mazzarelli et al., 2015). In addition, we may hypothesise a further ontogenetic window of vulnerability linked to the onset of pleopod development. In *P. serratus*, larval observations indicate increased sensitivity at stage 3, just before the transition to zoea 4, which coincides with the first appearance of pleopods. A comparable pattern could occur in *P. longirostris* between stages 2 and 3, with pleopods emerging at stage 3. The ontogeny cost of forming these appendages, together with the associated reorganisation of locomotor and possibly respiratory functions, is likely to be substantial and could transiently exacerbate energetic and osmotic stress, thereby increasing sensitivity at this developmental stage. As larval acclimation occurs within hours (Charmantier, 1998), the low initial hazard and subsequent stabilisation of survival at 20–30 PSU in our data are consistent with rapid osmotic adjustment. By contrast, the sustained losses at 10 PSU

suggest a capacity limit rather than an acclimation lag. Similar patterns of molting difficulties at low salinities have previously been reported for *P. longirostris*. González-Ortegón et al. (2016) observed 0% survival at 5 PSU, with the larvae being unable to moult to the second zoeal stage. Similarly, Antonopoulou and Emson (1989) reported total mortality at this salinity. These findings highlight the significant energetic demands of osmoregulation under extreme osmotic stress, which can interfere with other vital physiological processes and ultimately result in mortality. These observations highlight the importance of synchronising the development of osmoregulatory systems with prevailing environmental conditions for the successful growth and survival of decapod larvae. Furthermore, the cumulative impact of salinity throughout development is reflected in metamorphosis success; higher salinities are generally associated with higher metamorphosis rates. In *P. longirostris*, González-Ortegón et al. (2016) reported survival rates of around 70% at 20 PSU and 18 °C. In contrast, Feuillassier et al. (2012) observed nearly 50% mortality during the second week post-hatching when conducting larval rearing throughout the egg-laying period in a single tank maintained at 15 PSU and 20 °C. By contrast, in our study, 50% mortality at 15 PSU was only observed in female 3 after 18 days of development. While this difference may reflect variations in maternal provisioning or population (Holm, 1990), we did not quantify genetic structure or maternal traits in these cohorts. Therefore, we present this explanation as a plausible hypothesis alongside the possibility of methodological differences between studies (e.g. density, feeding, and water renewal).

#### 4.3. Larval fitness at metamorphosis: body mass and growth rate as performance indicators

The size or mass of the larvae and the energy allocated by the female to her offspring (i.e. per-offspring investment, or POI) at certain stages determines their performance (Marshall and Keough, 2008; Oliphant and Thatje, 2013; Baudet et al., 2024). In decapod larvae, an increase in the number of moults (and therefore development time) at a constant temperature is generally associated with a higher mass of juveniles at metamorphosis (*Chasmagnathus granulata*: Giménez and Torres, 2002; *Palaemon varians*: Oliphant et al., 2013; *P. serratus*: Baudet et al., 2024). The greater the mass of juveniles at metamorphosis, the better their fitness (Anger, 2003; Oliphant et al., 2013; Baudet et al., 2024). Prolonged development time may therefore play an important role in larval mass gain by delaying metamorphosis (Baudet et al., 2024). In the experiment, larvae under the most stressful conditions of 10 and 15 PSU took longer to develop, but this was not reflected in their weight gains or weight at metamorphosis (Figs. 6 and 7). The effects of low salinity appear to cause osmotic stress throughout larval development, which larval plasticity does not fully compensate to improve juvenile fitness. While there was no consistent reduction in juvenile mass or weight gain in larvae with an additional instar, this cohort was small ( $n = 9$ ) and was found in only one female. Therefore, this result should be interpreted cautiously and viewed as preliminary. However, a trend does seem to emerge from the results. In our study, juveniles had a greater mass at metamorphosis with higher salinity, with an average weight ranging from 1.85 mg to 2.23 mg for salinities of 10 to 30 PSU, respectively. This increase in mass at metamorphosis is reflected by a progressive increase in weight gain per day, which is greater for larvae in higher salinity conditions. Indeed, larvae subjected to lower salinities experienced weight gains of 0.065 mg per day versus 0.094 mg per day for salinities of 10 to 30 PSU. Changes in growth in response to salinity variations may indicate whether food intake or conversion is affected by salinity (Anger, 2003). We propose that the link between feeding and growth at low salinity is a plausible hypothesis, informed by analogous decapods (e.g. *Pandalus borealis* and *Cancer irroratus*), in which salinity stress suppresses feeding. Targeted assays of ingestion or growth potential at 10–15 PSU would be required to confirm this mechanism in *P. longirostris* (Anger, 2003).

#### 4.4. Developmental pathway and fitness responses to salinity in *P. longirostris* larvae

Overall, the developmental pattern of the larvae does not appear to be affected by salinity or *ad libitum* feeding at 18 °C. Although a supernumerary stage was observed in the early developmental stages, the small number of individuals observed (only in one female) does not allow us to formally conclude that the larvae in this experiment exhibit plasticity by adopting an alternative developmental pathway. Taken together, these patterns suggest that salinity determines the pace and outcome of the early development of *P. longirostris*. There is an operational window of 20 to 30 PSU, with peak performance occurring near 25 PSU. At 10–15 PSU, however, prolonged development and lower metamorphic success suggest that developmental plasticity only partially offsets osmotic and energetic costs. At  $\geq 20$  PSU, rapid acute adjustment likely stabilises survival and enhances carryover condition (*i.e.* juvenile mass and daily gain). These thresholds provide a basis for evaluating nurseries and offer practical guidance for managing freshwater inflows during the larval season. They also establish the necessary baseline to test how co-drivers (temperature and food availability) shift or compress this window. Although developmental plasticity is well documented in the *Palaemonidae* family, our dataset does not demonstrate compensatory plasticity in response to salinity. The supernumerary pathway was rare and this prevents robust inference. Furthermore, if prolonged development at low salinity were compensatory, we would expect to see heavier juveniles. However, juvenile mass and daily mass gain did not increase at 10–15 PSU. We therefore treat plasticity as a plausible but unconfirmed mechanism and as a limitation of the present dataset. To capture plastic responses more directly, future work should consider pairing staging with biochemical and energetic endpoints (*e.g.* lipid and protein content, glycogen, RNA:DNA and C:N ratios) and scope for growth. It should also consider routine metabolic rate and, where feasible, ingestion/absorption efficiency and  $\text{Na}^+/\text{K}^+$ -ATPase activity across salinities.

Of the two main larval dispersal strategies described for estuarine species, the retention of larval stages within the estuary, and the export of newly hatched stages into coastal shelf waters, with a subsequent return of later larval or post-larval stages, *P. longirostris* appears to follow an intermediate strategy (Sandifer and Smith, 1979; Strathmann, 1982; Bilton et al., 2002). This flexible approach enables larval development to occur in either the lower estuarine regions or the neritic zones, depending on the specific features of the estuary, such as the outflow of freshwater and the dynamics of the adjacent coast (Paula, 1998; Queiroga, 1996). Given the improved performance at  $\geq 20$  PSU, it is plausible that larvae are exported towards higher-salinity coastal waters. With a larval duration of around 20 days in *P. longirostris*, larval dispersal over distances of several kilometres is possible, which could facilitate the exchange of larvae between neighbouring estuaries. As our study did not track dispersal or analyse genetics, we present connectivity as a working hypothesis rather than a demonstrated outcome (Palumbi, 2003; Levin, 2006; Cowen and Sponaugle, 2009).

## 5. Conclusion

In controlled laboratory conditions and across a five-level salinity gradient, our data suggest that the operational window for larval development in *P. longirostris* is 20 to 30 PSU, with optimal performance near 25 PSU and reduced performance at 10–15 PSU (slower development, lower metamorphosis and poorer juvenile condition). Due to the small number of supernumerary cases and the single-factor design, these thresholds should be considered provisional estimates rather than being applicable to the whole species. Additionally, our dataset provided limited evidence for compensatory plasticity. Future factorial experiments (salinity x temperature/food) coupled with physiological and biochemical markers (*e.g.* hemolymph osmolality,  $\text{Na}^+/\text{K}^+$ -ATPase/V-ATPase activity, ion transporter expression, metabolic rate and lipid,

protein and glycogen reserves) would determine whether co-drivers shift the optimum or compress tolerance. Replication across females and populations and field validation (*e.g.* coupling performance functions to hydrodynamic transport/recruitment models) will be essential to assess the generality and ecological significance of the reported thresholds.

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## Availability of data and material

The data are freely available upon contacting the authors.

## CRediT authorship contribution statement

**Jason Jeanne:** Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Jean-Baptiste Baudet:** Writing – original draft, Methodology, Conceptualization. **Benoît Xuereb:** Writing – original draft, Supervision, Funding acquisition, Conceptualization. **Aurélie Duflot:** Writing – original draft, Investigation. **Agnès Poret:** Investigation. **Céline Boulangé-Lecomte:** Writing – original draft, Supervision, Funding acquisition, Conceptualization. **Romain Coulaud:** Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

## Consent for publication

All authors have given their consent for the article to be published.

## Ethics approval

All authors declare that the work described has been carried out in accordance with EU Directive 2010/63/EU for animal experiments.

## Funding

This study was supported by the Normandie Region and the European Maritime and Fisheries Fund (Action 28 “Partnerships between scientists and fishermen”; GeDuBouq project).

## Declaration of competing interest

All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

## Acknowledgements

We would like to thank the Thalasso of Deauville for the supply of natural seawater and the University of Le Havre for the facilities and the FR 3730 CNRS SCALE, a federative structure for environmental science research in the Normandy region.

## Data availability

Data will be made available on request.

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