

Estimating the life-history parameters of the white prawn, *Palaemon longirostris* (Crustacea: Palaemonidae), in a temperate European estuary

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Abstract

Life history parameters are indicators of stock structure and for the dynamics of biological populations. In this work, we examine multiple life-history parameters (size distribution, growth, mortality, and longevity) of *Palaemon longirostris* H. Milne Edwards, 1837 inhabiting the estuarine temperate waters of the Guadalquivir estuary through size-frequency distribution data obtained from June 1997 to May 1999. Sexual dimorphism in size was evident, as females displayed a larger body size than males. The carapace length-weight relationship indicated a negative allometric growth pattern in both sexes. Additionally, the growth performance index indicated a higher value for females ($\Phi = 2.50$) compared to males ($\Phi = 2.33$). The recruitment pattern analysis of *P. longirostris* indicated that females experienced a greater recruitment rate from March to August, while males exhibited a higher recruitment rate between April and July. Our study found that natural and fishing mortality rates were similar among male *P. longirostris*, whereas fishing mortality had a smaller effect on the overall mortality of females. The exploitation rates for both male and female stocks were optimally balanced. These findings, more than increasing our understanding of the life-history strategies of *P. longirostris*, garner data used to understand the ongoing effects of climate change upon this species.

Introduction

Functional relationships between the estuarine environment and commercial shrimp resources are well known worldwide (Darnell, 1990). Estuaries are critical habitats with high shrimp productivity due to their capacity as nursery grounds and nutrient sources. Estuaries have large mesozooplankton populations of detritivorous consumers, which serve as food for shrimp species (Elliott et al. 2002; González-Ortegón et al. 2010). The ecological importance of shrimps and prawns is demonstrated through biology and population dynamic studies of palaemonid, penaeid and crangonid species of commercial interest in various estuaries (Siegel et al., 2005). Estuaries can be considered as natural farms for shrimp species that complete their life cycle, and these habitats are identified as integrated systems for fisheries (Meynecke et al., 2007; Gonzalez-Ortegon et al., 2015; de Carvalho-Souza et al., 2019). Among shrimp species, within European estuaries, species of the genus *Palaemon*, such as *P. serratus*, *P. varians* and *P. longirostris* are the main species of commercial interest in Europe (Holthuis, 1980). *Palaemon* Weber, 1795 with six species, including one non-indigenous species in European waters (González-Ortegón and Cuesta 2006), is one of the most commercially important genera of Palaemonidae Rafinesque 1815 (Holthuis, 1980). The white prawn *Palaemon longirostris* H. Milne Edwards, 1837 is an estuarine species that complete their entire life cycle in brackish waters (González-Ortegón et al., 2006; 2010; Béguer et al., 2010). This species has a wide geographical native range along the North Atlantic coast, spanning from northwestern Germany and north Wales to North Africa in Morocco (González-Ortegón and Cuesta 2006; González-Ortegón et al., 2016; Taybi et al., 2021). Within this zone, it is also found in the Netherlands, Baltic Sea, France, and Portugal (Van den Brink and Van der Velde, 1986; Cartaxana, 2003; Grabowski, 2006; Béguer et al., 2010). Its presence is limited in the Mediterranean Sea, being found on the western area in the Guadiaro (Spain), Molouya (Morocco), and Miliana (Tunisia), and on the eastern side –

although not all reports are confirmed – including in Egypt, Turkey, Israel, and the Black Sea (Zariquiey Álvarez, 1968; D'Udekem d'Acoz, 1999; Sezgin et al., 2007). This species is considered a key species in the trophic dynamics of European estuaries (Moreira et al., 1992; González-Ortegón et al., 2009).

In European waters, various studies on the biology of *P. longirostris* have focused on its population dynamics, distribution, ecophysiology, feeding habitats, larval ecology and migration (Van Den Brink and Van der Velde, 1986; Campbell, 1988; Paula 1988; Cartaxana, 1994; 2003; González-Ortegón et al., 2006; 2009; Béguer et al., 2010; 2011; 2012). Reproductive studies have been undertaken in the Mira River estuary in Portugal (Cartaxana, 2003) and Gironde estuary in France (Béguer et al., 2012). In the Guadalquivir River estuary, the estuarine species *P. macrodactylus* and *P. longirostris* are the dominant species in terms of density meanwhile the native *P. varians* coexists in their canals and estuarine marshes, both with a physiological capacity to permanently dwell (González-Ortegón et al., 2006). The interaction between the exotic oriental shrimp, *Palaemon macrodactylus* Rathbun, 1902 and *P. longirostris* indicated a strong trophic overlap both having mysids as their main prey (González-Ortegón et al. 2009). In the saltmarshes, *P. longirostris* is not found and the native *P. varians* coexists with that exotic counterpart species and is not affected by the presence of this potential competitor, despite high diet similarity (Gonzalez-Ortegón et al., 2015).

The shrimp fishery in estuaries such as the Guadalquivir estuary of the Atlantic coast of Europe indicates the value of these species as a resource for fishermen in the area (Sobrino et al., 2005). This estuary plays an important hydrological and ecological role in the southernmost part of the Atlantic coast of Europe, serving as an essential habitat and nursery ground for many aquatic species (González-Ortegón et al., 2015; de Carvalho-Souza et al., 2019), including commercially important decapod crustaceans such as shrimps and prawns (*Crangon crangon*, *Penaeus kerathurus*, and *Palaemon* spp.) (Cuesta et al., 2006; González-Ortegón et al., in review).

Life history parameters are indicators for the dynamics of biological populations and the study of these traits are relevant to assess natural and anthropogenic effects. The effects of natural and human-controlled freshwater inputs in estuaries such as the Guadalquivir modified the physico-chemical conditions and consequently biological production and estuarine lower trophic levels (Gonzalez-Ortegón and Drake, 2012). The assessment of biological changes in an ecosystem caused by anthropogenic alterations can be assessed through life-history parameters. The ecological study of the life-history parameters during two years in the Guadalquivir estuary would provide relevant information for the biological response of one of its the dominant estuarine species *P. longirostris* because they are phenotypic expressions of the interaction between genotypic and environmental influences.

So, we utilized length frequency methods to estimate the life-history parameters of *P. longirostris* individuals collected in 1997–1999. This unique dataset represents the first data available from the Guadalquivir River estuary. This approach is an outstanding opportunity to acquire baseline data on the population production.

Material and Methods

Study area and sampling

Monthly samplings were carried out at the Guadalquivir river estuary (SW Spain: 36°45' – 37°15' N, 6°00' – 6°22' W), between June 1997 and May 1999, at five sampling stations (Bonanza, La Esparraguera, Tarfía, La Mata and La Horcada) situated 50, 40, 32, 20, and 8 km upstream from the river mouth (Fig. 1). Samplings were conducted from a boat anchored on the east bank of the estuary at a water column depth of approximately 3 m during the low tide. Four samples were collected over a 24-hour period during the new moon phase at each sampling site. Passive hauls were used to collect samples during the first two hours of each diurnal and nocturnal flood and ebb tide. The samples were collected with three nets working in parallel, each constructed with a 1 mm polyamide gauze mesh and an opening of $2.5 \times 3 \text{ m}^2$. The nets were approximately 10 m long. The total catch was placed in a calibrated container, and the volume was estimated. About thirteen liters of the collected material, or the entire volume, if smaller, was randomly sampled and preserved in 10% formalin. In the laboratory, the individuals were sorted into species and counted. After, total length (TL), carapace length (CL) and total weight (W) were measured to the nearest 0.01 mm and 0.01 g, respectively.

Data analysis

The distribution of white prawns was determined through the analysis of size frequency distribution using 0.5 mm size intervals. The sex of the individuals was based on the presence (males) or absence (females) of an appendix masculine on the second pleopod, and the sex ratio was calculated (F: female, M: male). Chi-square tests were used to evaluate whether there was a significant deviation from the 1:1 sex ratio with a significance level of 0.05.

The length–weight relationship was estimated using the equation: $W = aCL^b$ (Le Cren, 1951), where W is the total weight (g), CL is the carapace length (mm), a is the intercept, and b is the slope of the relation. The allometric condition b of each body structure was evaluated, which corresponded to isometry (b = 1), negative allometry (b < 1), or positive allometry (b > 1), using Student's t-test ($H_0: b = 1, \alpha = 0.05$) (Zar, 1996).

The Von Bertalanffy growth model (VBGM) (Von Bertalanffy, 1938) was used to estimate the growth. The VBGM function is $LT = L_{\infty}(1 - e^{-K(t - t_0)})$, where LT represents the total length at time t, L_{∞} is the asymptotic total length, K is the instantaneous growth coefficient, and t_0 is the hypothetical age when the specimens had an average length of zero (Hilborn and Walters, 1992). To estimate the input values for the L_{∞} parameters, the Powell-Wetherall method was used (Powell, 1979; Wetherall et al., 1987). Growth performance comparisons were conducted using the growth performance index (Φ), which is preferred over the individual uses of L_{∞} and K (Pauly and Munro, 1984). The index was calculated as follows: $\Phi = \log(K) + 2\log(L_{\infty})$. The growth parameters were fitted separately for each sex.

The recruitment pattern was estimated using length-frequency data, with asymptotic length (L_{∞} in mm) and growth coefficient (K in year^{-1}) as input data. This method reconstructs recruitment pulses based on monthly length frequencies, providing information on relative peak recruitment per year (Pauly, 1987).

To estimate the natural mortality (M), total mortality (Z), fishing mortality (F), and exploitation rate (E), we utilized the most recent formula based on a meta-analysis conducted by Then et al. (2015). Mortality and longevity were calculated using the parameters derived from the Von Bertalanffy growth model. All analyses were performed using the R software version 4.3.0 (R Core Team, 2023) and TrofishR (Mildenberger et al., 2017).

Results

Size, Length frequency distribution and Sex-ratio

A total of 19,926 individuals (375 juveniles, 7,826 females and 9,003 males) were measured in the 24 samplings (Fig. 2 and Table 1). Size of individuals ranged from 0.5 to 19.1 mm with mean of 6.67 ± 2.53 mm CL. The female specimens had larger sizes (range, 2.51 to 19.1 mm), showed a mean CL of 7.1 ± 2.62 mm and those from males 6.1 ± 1.34 cm (range, 2.68 to 11.7 mm) (Fig. 3). The months that presented the largest sizes were between November-February and June for females, and November-December and May-June for males (Figure S1).

Female-biased sex ratios for *P. longirostris* were observed in December, January, February, and March, whereas male-biased sex ratios were observed from August to November and peaked in April and May.

Table 1

The monthly range (Min. – Max.), mean total length (mm) \pm SD, and sex ratio of females and males of *P. longirostris* from June 1997 to May 1999. Significant values ($P < 0.05$ *, $P < 0.001$ **, and $P < 0.0001$ ***) are presented for each sex ratio.

Date	Females				Males				Sex ratio (F:M)
	Min.	Max.	Mean	SD	Min.	Max.	Mean	SD	
jun-97	2.51	14.05	6.26	1.72	3.36	8.55	5.28	0.81	1:1.16*
jul-97	3.03	10.46	6.14	1.89	3.13	8.84	5.49	0.84	1:1.87***
ago-97	2.91	11.48	6.09	2.15	2.68	9.28	5.45	1.01	1:1.36***
set-97	3.01	11.50	5.98	2.17	3.03	8.33	5.78	1.18	1:1.21**
out-97	3.00	12.44	6.96	2.53	3.19	9.78	6.31	1.23	1:1.20**
nov-97	3.10	17.16	8.37	2.57	3.50	10.22	6.72	1.37	1:1.13*
dez-97	3.97	13.86	9.79	2.14	3.78	10.04	6.53	1.24	1:0.64***
jan-98	3.50	15.68	9.81	2.38	3.14	9.80	6.44	1.49	1:0.67***
fev-98	5.46	14.75	9.94	2.07	4.18	9.43	6.58	1.38	1:0.45***
mar-98	3.50	13.97	9.21	2.45	3.50	9.85	6.89	1.21	1:0.64**
abr-98	5.20	14.60	10.54	2.47	4.03	9.86	7.51	0.99	1:3.43***
mai-98	3.00	11.38	3.70	0.71	3.05	10.04	5.27	2.26	1:0.38***
jun-98	3.16	14.75	6.14	2.08	3.32	10.20	5.50	1.49	1:0.91
jul-98	3.00	11.56	5.30	1.47	3.05	9.41	5.24	1.13	1:0.92
ago-98	3.50	12.94	6.56	1.22	3.50	9.70	5.67	0.88	1:1.15*
set-98	3.00	11.23	6.52	1.93	3.00	9.29	6.01	1.06	1:1.28***
out-98	3.00	11.50	6.87	2.22	3.30	9.30	6.12	1.25	1:1.21**
nov-98	3.00	12.48	7.58	2.72	3.00	10.40	6.31	1.51	1:1.23**
dez-98	3.30	19.10	8.51	2.50	3.50	11.70	6.75	1.38	1:1.12
jan-99	3.50	13.80	9.23	2.50	4.10	10.40	7.09	1.18	1:1.19*
fev-99	4.00	15.30	9.77	2.16	3.97	10.00	7.28	1.17	1:0.99
abr-99	3.67	12.97	8.21	2.23	4.30	9.35	6.80	1.06	1:1.30*
mai-99	4.00	12.07	7.31	2.01	4.85	9.97	6.96	1.03	1:2.07***
	5.12	11.40	7.65	1.65		9.36	7.00	1.02	1:4.03***
Total	2.51	19.1	7.1	2.62	2.68	11.7	6.1	1.34	1:1.15*

Length-weight relationship (LWR)

The relationship between carapace length and weight indicated negative allometric growth in both sexes (Fig. 4).

In both cases, the exponents of the equation indicated allometric growth ($b < 3$). However, while the difference found at the cut-off point with the slope was not statistically significant ($t = 1.24$; $gl = 715$; $P > 0.05$), the difference was significant for the intercept ($t = 1.16$; $gl = 715$; $P < 0.05$), indicating that after a certain size, males weighed more than females of the same size.

Von Bertalanffy Growth Parameters and Recruitment

The growth parameters of each sex were estimated using von Bertalanffy growth models, and the results showed that females had higher values of L_{∞} and K ($L_{\infty} = 15.11$, $K = 1.39$) than males ($L_{\infty} = 12.66$, $K = 1.35$), as well as a greater growth rate with age (Fig. 5A-B and Figure S2A-B). In relation to the growth performance index, females exhibited a higher growth performance index ($\Phi = 2.50$; Figure S2A) than males ($\Phi = 2.33$; Figure S2B). The R_n value, which is a goodness-of-fit index, was 0.137 for females and 0.177 for males.

The recruitment pattern of *P. longirostris* showed that females had higher recruitment between March and August, whereas males had higher recruitment between April and July, with peaks in June and May (Fig. 6), respectively. It appears that recruitment can occur throughout the warm months of the year, indicating a seasonally continuous pattern for females. In contrast, males are primarily recruited during spring and early summer.

Mortality and Longevity

Natural mortality rates (M) were estimated as 2.13 and 2.21 year^{-1} for females and males, respectively. The estimated values of the total (Z) and fishing (F) mortality rates, longevity and the exploitation rate (E) by sex are presented in Table 2.

Table 2

Estimates of natural mortality ($M\text{-year}^{-1}$), total mortality ($Z\text{-year}^{-1}$), fishery mortality ($F\text{-year}^{-1}$), exploitation rate (E), and longevity (Long. year^{-1}) through the Length-Converted Catch Curve fitted for females and males of *P. longirostris* in the Guadalquivir estuary.

Method	M	Z	F	E	Long.
Females	2.13	3.74	1.25	0.33	2.38
Males	2.21	7.37	2.37	0.32	2.36

Discussion

This study enabled the analysis of life-history parameters in both male and female populations of *P. longirostris* in the Guadalquivir River estuary. The frequency of individuals at all stages of development throughout the study provides evidence that *P. longirostris* is capable of successfully completing its life cycle within the estuary (González-Ortegón et al., 2012).

For *Palaemon longirostris*, as well as in other species of *Palaemon*, a consistent finding reveals that females exhibit larger sizes compared to males, which aligns with the findings of the present study. This trend has been observed in *P. adspersus* Rathke, 1836 and *P. elegans* Rathke, 1836 (Berglund, 1983; Vejan et al., 2022), *P. gravieri* (Yu, 1930) (Kim, 2005), *P. xiphias* (Risso, 1816) (Guerao et al., 1994), and other populations of *P. longirostris* (Van Den Brink and Van Der Velde 1986; Cartaxana, 2003, Béguer et al., 2010).

This sexual dimorphism may be associated with the reproductive biology, as an increase in carapace length indicates a capacity to produce more oocytes, with a consequent increase in fecundity (Van Den Brink and Van Der Velde, 1986; Cartaxana, 2003, Béguer et al., 2010). On the other hand, the sex ratio in *P. longirostris* populations was usually in favor of males. However, during cold periods characterized by low temperatures, the occurrence of the lowest densities for both sexes, as well as a more balanced sex ratio between males and females among adults, suggests a potential association with the initiation of the reproductive period.

When comparing the reproductive period of *P. longirostris* in the Guadalquivir River estuary with other European estuaries (Sorbe, 1983; Van Den Brink and Van Der Velde, 1986; Cartaxana, 1994; Béguer et al., 2010), notable differences emerge. In the southern regions, the reproductive period appears to commence earlier and endure longer than in the northern regions, with the Guadalquivir River estuary exhibiting an even lengthier reproductive period than the Mira River in Portugal (Cartaxana, 1994). Both estuaries display a primary reproductive peak in spring (March-April), with the Guadalquivir estuary additionally featuring another peak in summer.

The juveniles grow in the estuary during the warmest season, where they tend to gather predominantly in the oligo-mesohaline waters found near the mouth of the estuary. Our results on recruitment patterns revealed that during warm periods, the lowest average size of males and females was observed, which can be attributed to the incorporation of new recruits. However, due to the growth observed between spawning periods, the average sizes of males and females showed clearer variations.

The growth of *P. longirostris* exhibited a negative allometry, as indicated by a b-value of < 3 . This suggests that the rate of weight gain did not match the rate of increase in length along the curve depicting the relationship between total length and body weight. Our CL-W relationships were similar between sex categories (b-value of 2.86 for females and 2.96 for males). However, when compared with Cartaxana (2003) (b-value of 2.88 for females and 3.09 for males) and Béguer et al. (2010) (b-value of 2.36 for females and 2.59 for males), slight differences were observed.

A comparison of the growth parameters of *Palaemon longirostris* in different estuaries is shown in Table 3. Furthermore, when making comparisons, it is recommended to use the growth performance index (Φ) instead of the intrinsic growth rates (K) (Pauly and Munro, 1984). Béguer et al. (2010) observed a higher Φ for the population in Gironde than that in the Mira River estuary. This observation suggests a link between the growth performance index and temperature. The temperature is also highlighted by González-Ortegón et al. (2009) as a potential primary factor governing the growth of estuarine species, including *P. longirostris* and the exotic oriental shrimp *P. macrodactylus*, in the Guadalquivir River estuary. The growth performance index of *P. longirostris* found in warm temperate waters exhibited similarities with other palaemonid species inhabiting similar latitudes (Oh et al., 2002; Kim, 2005), whereas in the Mira estuary, the Φ was lower than that of other species (Cartaxana, 1994). Previous studies conducted along different Spanish coastlines have reported relatively higher Φ values for *P. serratus* (3.84 – 3.96; Figueras, 1986), *P. xiphias* (3.59 – 3.97; Guerao et al., 1994) and *P. adpersus* (3.10–3.67; Manent and Abella-Gutiérrez, 2006).

Table 3

Comparison of the von Bertalanffy growth parameters fitted for females and males of *P. longirostris* in three European estuaries: the Mira River estuary (Cartaxana, 1994), Gironde River estuary (Béguer et al., 2011), and Guadalquivir River estuary (present study). K : growth constant; L_{∞} : asymptotic length; t_0 : age at $L(t_0)$; Φ : growth performance index.

		K	L_{∞}	t_0	Φ
Females	Mira River estuary	0.51	16.32	1.42	2.13
	Gironde River estuary	1.05–5.22	9.70-15.33	0.01–0.06	2.39–2.69
	Guadalquivir River estuary	1.39	15.11	0.22	2.50
Males	Mira River estuary	0.62	11.68	0.49	1.92
	Gironde River estuary	1.09–5.31	7.61–12.17	0.05–0.12	2.20–2.48
	Guadalquivir River estuary	1.35	12.66	0.17	2.33

Natural and fishing mortality rates in the Guadalquivir River estuary were comparable among males, whereas in the case of females, fishing mortality accounted for a relatively smaller proportion compared to other sources of mortality. The exploitation rates for both the male and female stocks were balanced, with values ranging from 0.32–0.33. This indicates that the stock was at an optimal level of exploitation in the period studied, where fishing mortality is equal to natural mortality or $E = (F/Z) = 0.5$ (Gulland, 1971). Growth parameters, and consequently mortality estimates, have the potential to exhibit spatial and temporal variation within a species, influenced by intrinsic (genetic) and extrinsic (environmental) factors, as well as geographic location, sex, and life stage (Fernandes et al., 2011).

Conclusions

We studied the life-history parameters of the white prawn, *P. longirostris* in the Guadalquivir River estuary and found important estimations among descriptors of size and length frequency distribution, sex-ratio, growth, recruitment and mortality for this population. Our findings reveal sexual dimorphism and allometric growth in *P. longirostris*. Recruitment patterns differ between genders, while mortality rates and exploitation exhibit gender-specific dynamics. The findings presented here holds valuable insights for future studies and fisheries stock management, as they contribute to a comprehensive understanding of the population dynamics of this species. This knowledge base serves as a reference point for ongoing surveys and facilitates a deeper comprehension of the impacts of environmental perturbations in the Guadalquivir River estuary.

Declarations

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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.

Data availability

Data will be made available on request.

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Figures

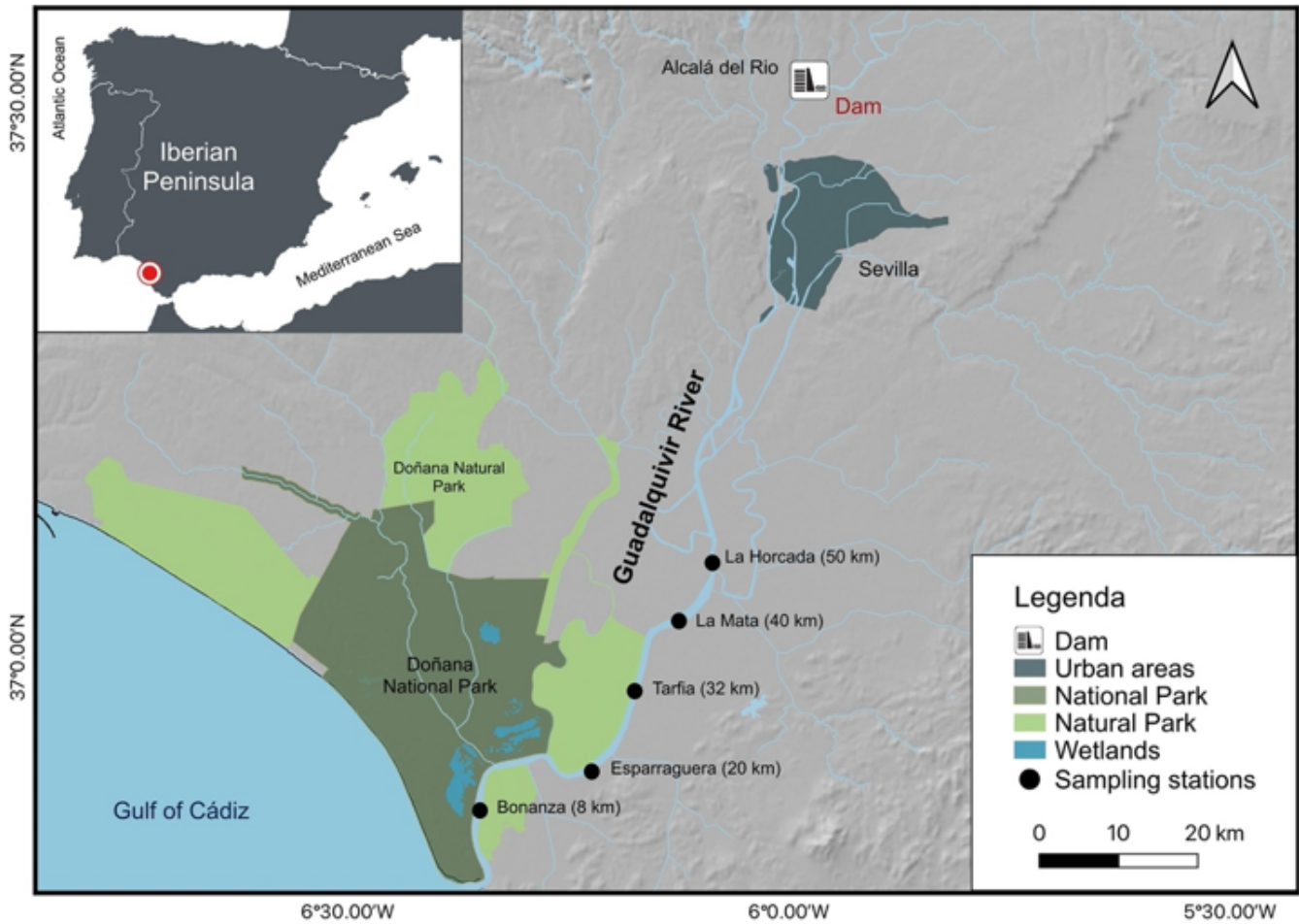


Figure 1

Map of the Guadalquivir River estuary and locations of the five sampling stations.

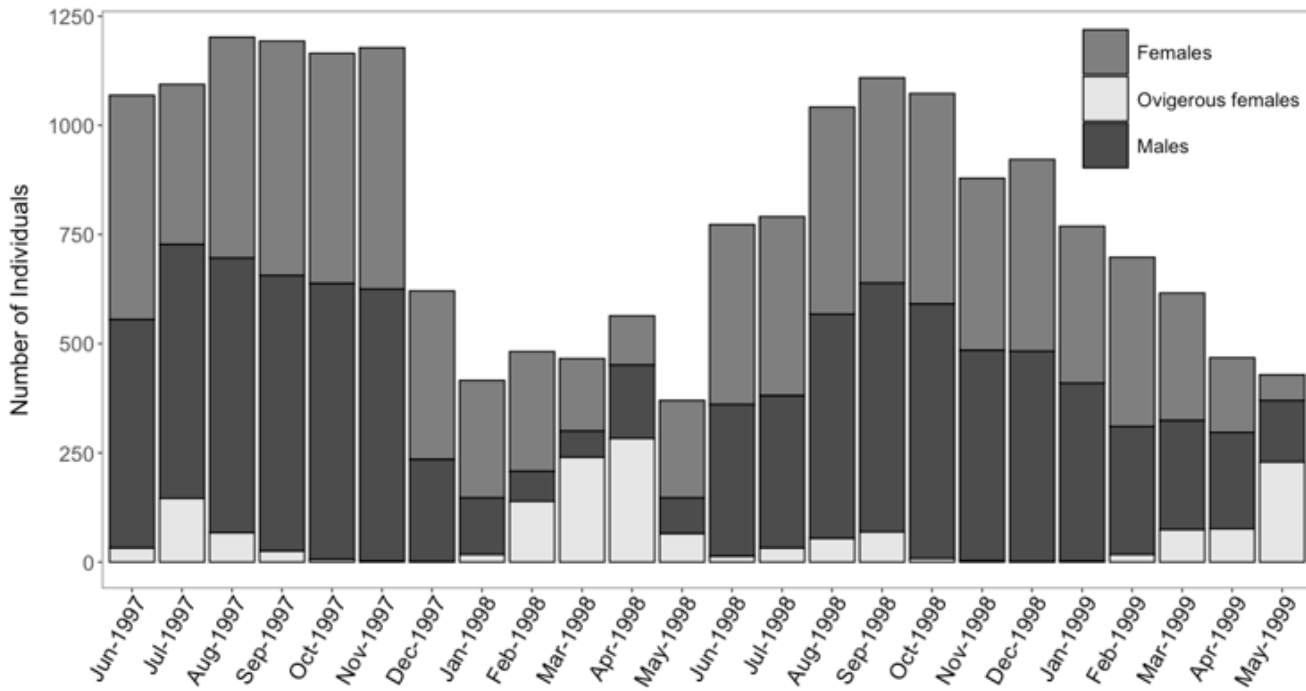


Figure 2

Number of individuals of females, ovigerous females and males of *P. longirostris* from the Guadalquivir River estuary (June 1997 - May 1999).

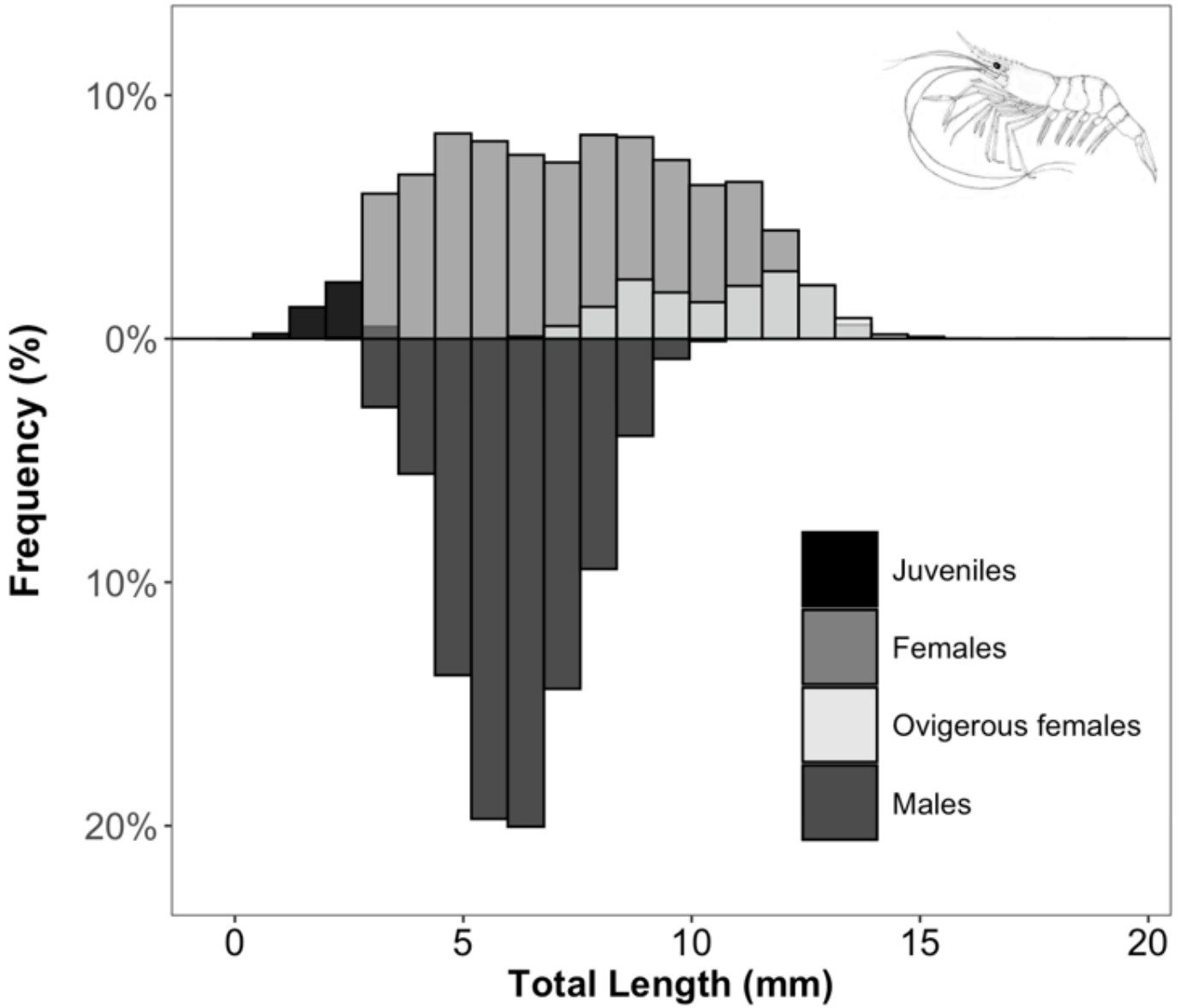


Figure 3

Length-frequency distributions of the white prawn *P. longirostris* from the Guadalquivir River estuary (1997-1999).

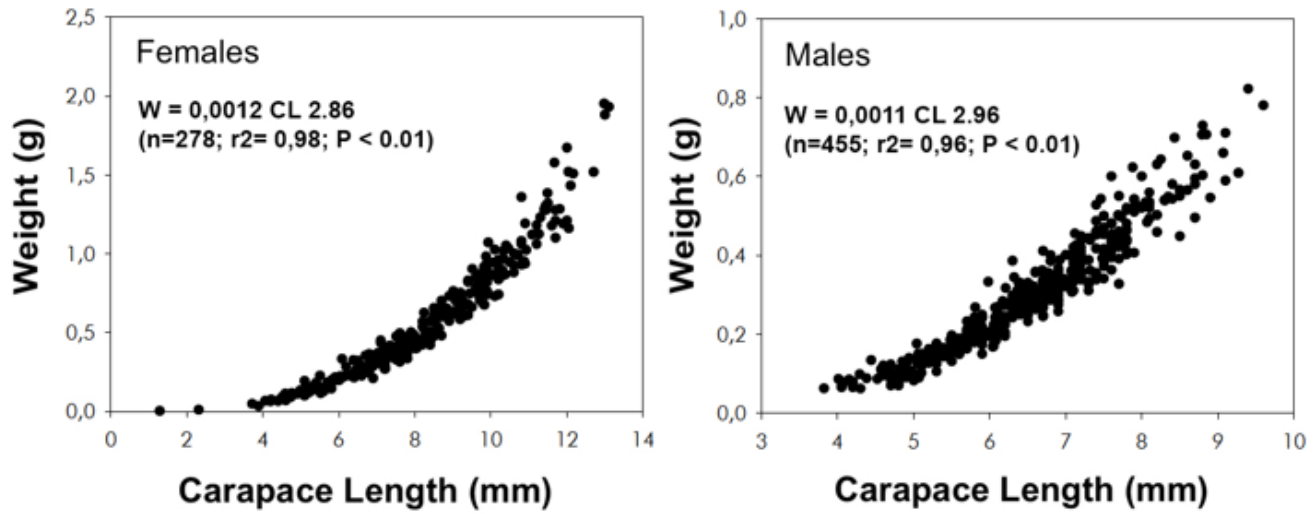


Figure 4

Relationship between carapace length (mm) and weight (g) for females and males of the white prawn *P. longirostris* from the Guadalquivir River estuary.

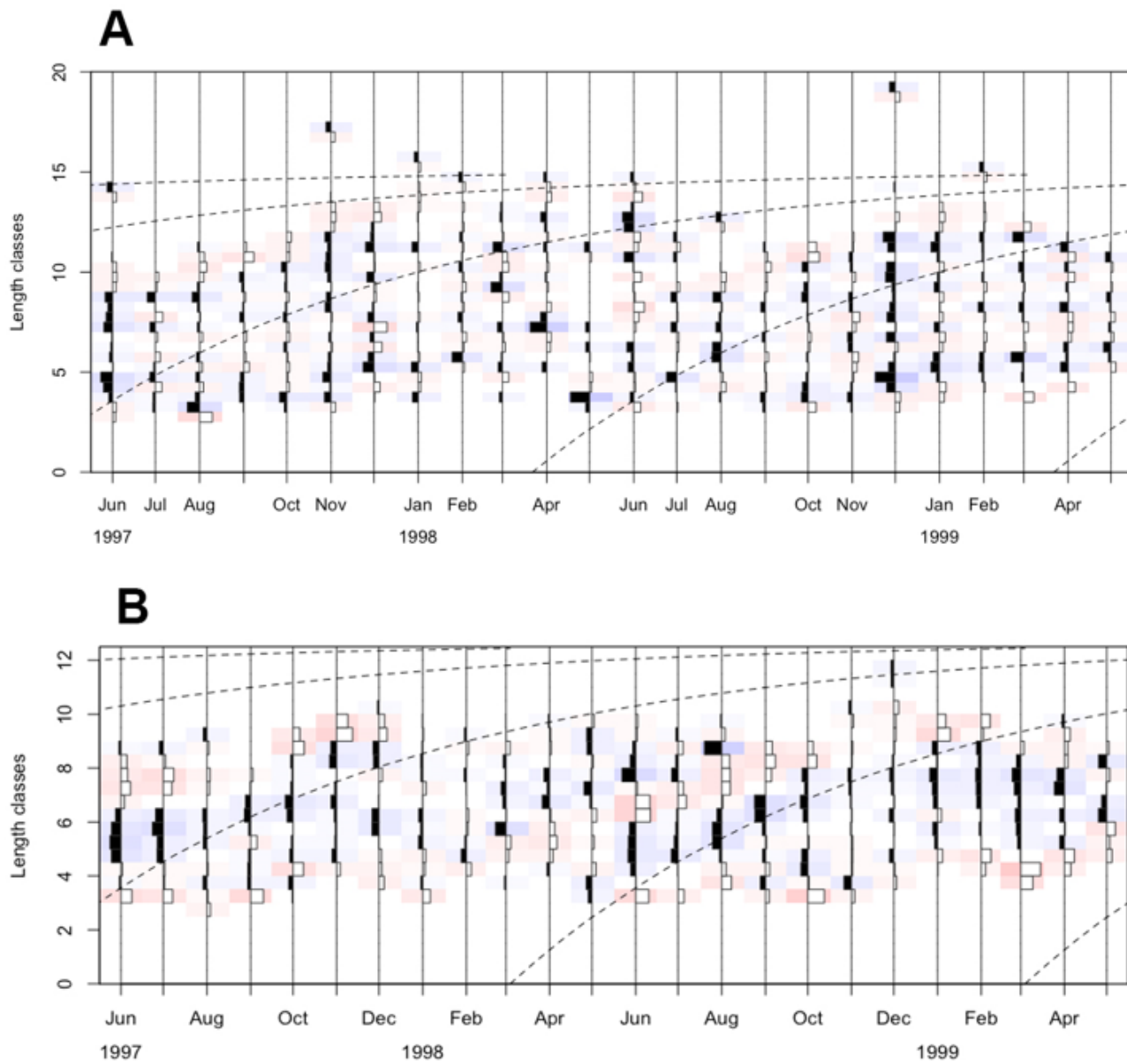


Figure 5

Length-frequency distribution data and the growth curves estimated using ELEFAN I (A) females and (B) males of the white prawn *P. longirostris* from the Guadalquivir river estuary (1997-1999).

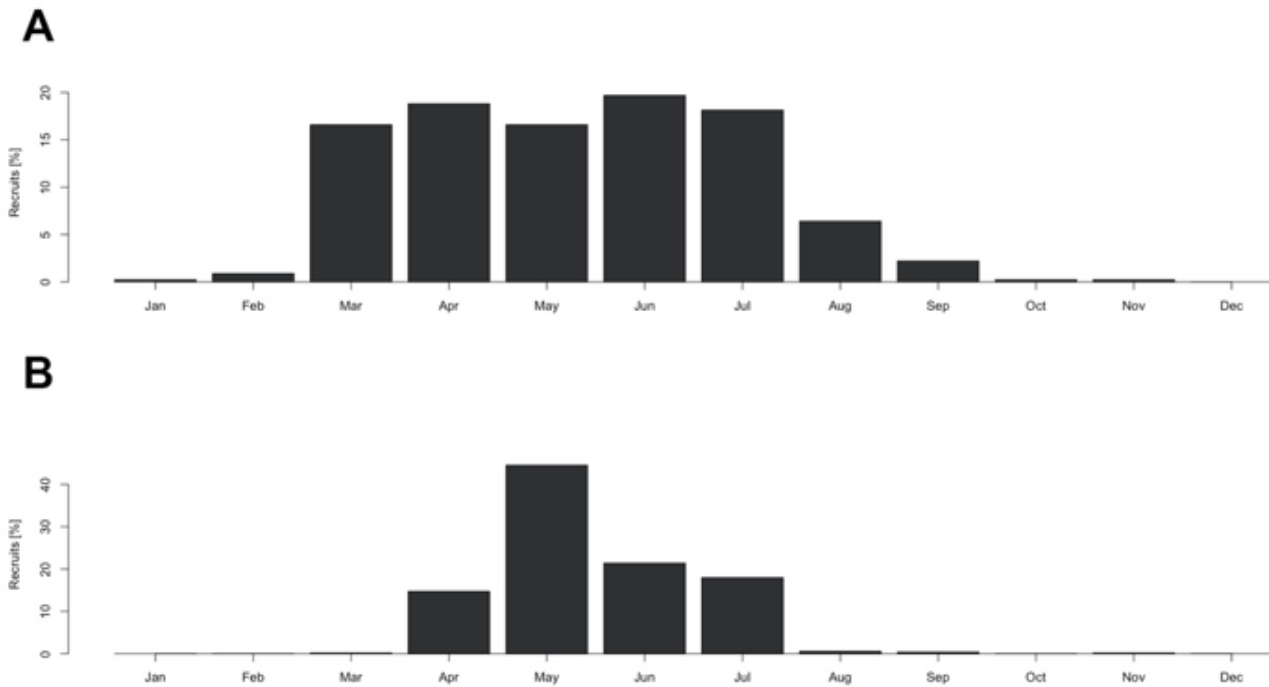


Figure 6

The percentual recruitment pattern of (A) females and (B) males of the white prawn *P. longirostris* from the Guadalquivir River estuary (1997-1999).

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