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ARTICLE

Ecology, life history and migration patterns of two key estuarine amphipods (*Gammarus chevreuxi* and *Corophium multisetosum*) in the Minho River (NW Iberian Peninsula)

Ecología, ciclo biológico y patrones migratorios de dos anfípodos estuarinos clave en el Río Miño (noroeste de la Península Ibérica)

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Abstract: Abundance and biomass of *Gammarus chevreuxi* and *Corophium multisetosum* were analysed monthly for one year, along the salinity gradient of the Minho River estuary. Both species were more abundant in the middle estuary with juveniles migrating upstream after the reproductive peaks (between late summer and early winter). After maturation, adults migrated downstream where optimal reproductive conditions were found. Subtidal sediments contained the majority of the populations with adult migrations occurring towards intertidal sediments during the summer. Densities for both species are much lower than in Ria de Aveiro, a estuary at a similar latitude. Unusually skewed sex ratios in favour of females were found prompting further investigation into the causes of this phenomenon.

Keywords: Amphipoda; Gammaridae; Corophiidae; estuarine ecology; life history

Resumen: Durante un año se analizaron mensualmente la abundancia y biomasa de los anfípodos *Gammarus chevreuxi y Corophium multisetosum* a lo largo del gradiente de salinidad del estuario del Río Miño. Ambas especies fueron más abundantes en la parte media del estuario, y los juveniles migraron río arriba depués de los picos reproductivos. Tras la maduración, los adultos migraron río abajo, donde se daban las condiciones óptimas para la reproducción. Los sedimentos submareales contenían la mayor parte de la población, y durante el verano se produjeron migraciones de adultos hacia los sedimentos intermareales. Las densidades de ambas especies fueron mucho menores que en la Ría de Aveiro, un estuario situado a una latitud similar. Se observó una proporción de sexos inusualmente sesgada a favor de las hembras, lo que motivará una investigación más profunda sobre las causas de este fenómeno.

Palabras clave: Amphipoda; Gammaridae; Corophiidae; ecología estuarina; historia de vida

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Supplementary information ↓

1. INTRODUCTION

Amphipods are abundant and ubiquitous in estuarine environments (Cunha *et al*., 1999; Marques & Bellan-Santini, 1990; Sousa *et al*., 2008). These crustaceans belong to the superorder Peracarida which is characterised by direct development without larval stages (Väiniölä *et al*., 2008). Embryos are carried in a brood chamber between pereopods (Väiniölä *et al*., 2008). They play an important role in nutrient cycling, feeding mainly on detritus (Guerra-García *et al*., 2014) and represent one of the main food sources for other high level consumers (Matthews *et al*., 1992; Mota & Antunes, 2012).

The amphipod *Gammarus chevreuxi* Sexton, 1913 is an epibenthic species, typical of Western European and North African estuaries, brackish lagoons and rias (Maren, 1975; Lincoln, 1979; Marques & Bellan-Santini, 1987, 1990; Dexter, 1992). It is commonly associated with low salinities, inhabiting the upper reaches of estuaries among macrophytes or on sandy, muddy and rocky bottoms (Lincoln, 1979; Subida *et al*., 2005). It is a grazer that may use dead roots and leaves as food (Subida *et al*., 2005). Populations of this species exhibit an iteroparous biannual life cycle, with an average lifespan of six months (Subida *et al*., 2005). In addition, the rate of maturation and the time between moults are strongly influenced by environmental variations in temperature and salinity (Sexton & Mathews, 1913; Sexton, 1924). Their abundance and biomass were found to be associated with variations in salinity, dissolved oxygen and chlorophyll a in the upper reaches of the Canal de Mira (Ria de Aveiro, Portugal), with maximum abundances occurring at lower temperatures (Subida *et al*., 2005). *Gammarus chevreuxi* exhibits nocturnal migratory behaviour during high tide floods, using water movement for displacement (Girisch *et al*., 1974; Girisch & Dennert, 1975). These migratory behaviours are cued by increases in salinity, water temperature and current velocity (Girisch & Dennert, 1975). From late summer to late spring juveniles migrate upstream and form the majority of the upstream population during these periods, while larger individuals migrate downstream to reproduce (Girisch *et al*., 1974; Girisch & Dennert, 1975). Temperature and photoperiod are important cues for sex determination in species of the genus *Gammarus* Fabricius, 1775 (Dunn *et al*, 2005). Female biased sex ratios can be observed in microsporidian parasitism, where infected females produce over 90% female broods (Terry *et al*, 1998).

The amphipod *Corophium multisetosum* (Stock, 1952) is a common estuarine species distributed along the European Atlantic coasts (Wijnhoven *et al*., 2011). It is usually found in brackish shallow waters, in a variety of substrates, typically burrowing in soft bottoms, avoiding silty and gravely-sized particles (Queiroga, 1990), or forming tubes in hard substrates (Wijnhoven *et al*., 2011). Populations have an iteroparous biannual life cycle, with a mean lifespan of six months (Cunha *et al*., 2000a). In addition, abundance is strongly influenced by environmental variations such as temperature and salinity (Queiroga, 1990; Cunha *et al*., 2000b). Its feeding behaviour is dependent on the concentration of phytoplankton in the water, adopting filter feeding behaviour at high concentrations and shifting to surface deposition feeding at low concentrations (Møller & Riisgård, 2006). Female biased sex ratios can also be observed for this species under microsporidian parasitism, where infected females produce mainly female broods (Mautner *et al*., 2007). The main goal of this study is to describe the life history and ecology of these two species in the Minho River estuary, focusing on three sections of the system (polyhaline, oligohaline and fresh-water) and different compartments (muddy and sandy bottoms and on macrophytes). In addition migratory patterns and sex ratios within these compartments of the estuary were also assessed.

2. MATERIAL AND METHODS

2.1 Study area

The estuary of the Minho River, located on the north-western border between Portugal and Spain, is a mesotidal partially-mixed system that tends towards a salt wedge during high floods (Sousa *et al.*, 2005). Salt intrusion typically extends up to 11 km and up to 17 km the summer (Mota & Antunes, 2012). Samples were collected in the lower estuary in a polyhaline section, in the middle estuary in an oligohaline section and upstream in a freshwater area (Fig. 1). Sampling was carried out on both subtidal and intertidal sediments. Intertidal sediment sampling was further subdivided into contiguous areas consisting of sand, muddy sand and sediment associated with macrophytes (*Zostera noltii*, *Juncus* spp. and *Egeria densa*).

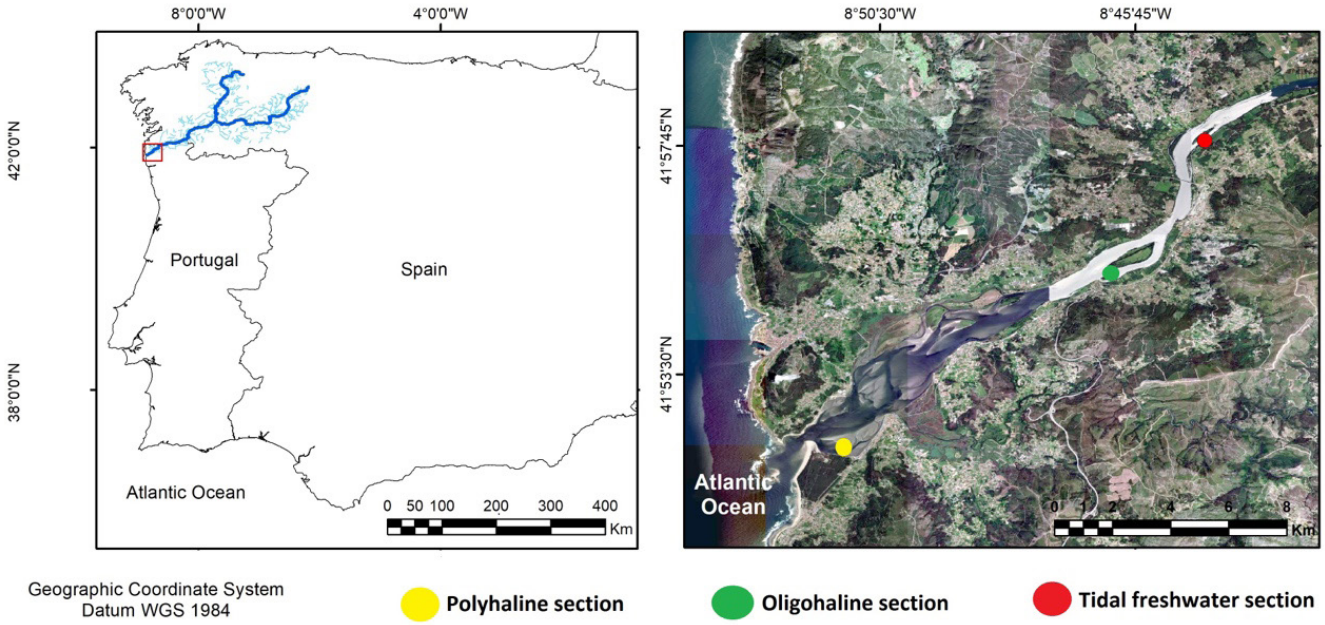

Figure 1- Study area.
Figura 1- Área de estudio

2.2 Sampling and laboratory procedures

Monthly sediment sampling was conducted from September 2021 to August 2022, at low tide during full moons. Subtidal sediment was collected using a Van Veen grab sampler with a grab area of 500 cm^2. Intertidal sediment was collected by delimiting 0.1 m^2 quadrats. Five replicates were collected for each sediment type. Sediment was sieved through a 500 µm mesh and bagged for laboratory analysis. An additional sediment sample was collected for texture characterisation and quantification of organic matter content. Environmental parameters were measured using a EUREKA Manta+35 multi-parameter probe. Water samples used for quantification of suspended organic matter were collected in the adjacent margins and from the bottom of the river using a Nansen bottle. One litre of sample water was filtered through a 47 mm diameter pre-weighed GF/C filter. The sediment and filters were dried at 60°C for 48 hours and then sieved through successively smaller meshes and weighed for texture characterisation. Four replicates of dry sediment and the dry filters were burnt in a muffle furnace at 550°C for 4 hours to quantify organic matter.

2.3 Data analysis

Individuals of each species were classified into four categories: juveniles, without distinctive morphological characteristics; males, with genital apophyses in the 7th pereonite; females, with oostegites and ovigerous females, carrying embryos; and then counted and measured for total body length, from the anterior margin of the head to the most distal part of the telson. Dry mass was determined by drying specimens at 60°C for 48 hours. Ash-free dry mass (AFDM) was determined by burning the dried samples in a muffle furnace at 550°C for 4 hours. Correlations between environmental parameters and amphipod abundance/biomass were determined using the non-parametric Kendall's rank correlation coefficient. A two way permutational multivariate analyses of variance (PERMANOVA) was used to test the effects of the temporal scale (in months) and of the sediment characteristics on the populations abundance and biomass. All analyses were performed using Past v4.10 software (Hammer *et al*., 2001).

3. RESULTS

3.1 *Gammarus chevreuxi*

The abundance and biomass of *Gammarus chevreuxi* were highest in the oligohaline section, followed by the freshwater environment, where slightly lower but still significant values were observed (Supp. file 1: Table S1). Furthermore, in polyhaline environments it was only found in March and April, on subtidal sandy sediments and intertidal muddy sediments with *Zostera noltii* Hornem., but its abundance was extremely low (2 individuals/m2) (Supp. file 1: Table S1). It was also less abundant in bare oligohaline and freshwater intertidal sediments (0 -6 individuals/m2) (Supp. file 1: Table S1). Therefore, subtidal environments and intertidal sediments with macrophytes such as *Juncus* spp. and *Egeria densa* shelter the majority of the population (Fig. 2). Furthermore, abundances and biomasses were mostly associated with subtidal sediments (Figs. 2; Supp. file 2: Figs. S1, S2). The two-way PERMANOVA analysis of abundance revealed that the habitat (PERMANOVA: $R2 = 0.22$, $F = 27.97$, $p<0.001$) and habitat/seasonal interaction (PERMANOVA: $R2 = 0.31$, $F = 1.86$, $p<0.001$) contributed the most to community variation, whereas seasonal variation (PERMANOVA: $R2 = 0.02$, $F = 0.04$, $p<0.001$) contributed to a lesser extent. Biomass variation follows the same patterns (habitat- PERMANOVA: $R2 = 0.24$, $F = 29.79$, $p<0.001$; season- PERMANOVA: $R2 = 0.04$, $F = 2.55$, $p<0.001$; interaction- PERMANOVA: $R2 = 0.29$, $F = 3.41$, $p<0.001$). Positive correlations were found between coarse sediment particles and *Gammarus chevreuxi* abundance or biomass, whereas negative correlations were found between fine sediments and sediment organic matter. Males tend to be larger (Supp. file 2: Figs. S3, S4, S5, S6, S7). Sex ratios were heavily skewed towards females (Fig. 3), which makes up approximately 80% of the total adult population. In oligohaline environments, juveniles were present throughout the year, with peaks in abundance occurring in November, whereas January and August have the lowest recorded abundances (Supp. file 2: Figs. S3, S4, S5, S6, S7). Overall, abundance and biomass for the whole population were highest in July (1284 individuals/m2; 0.26 gAFDW/m2) (Supp. file 1: Table S1). Ovigerous females were found between September and December, in February and between June and August (Fig. 3). Adults were absent from subtidal sediments in December and August, but a few individuals were observed in intertidal sediment with *Juncus* spp. (Fig. 3). In freshwater juveniles were the most abundant class, being absent between January and April, with peaks of abundance recorded in August, September and October (Supp. file 2: Fig. S5). No individuals were recorded here from February to April, while adults were absent from November to December and June to July. The leaves of *Egeria densa* and the intertidal sediment associated with this macrophyte have higher abundances of adult individuals, during periods when these populations disappear from the subtidal sediments (Fig. 3).

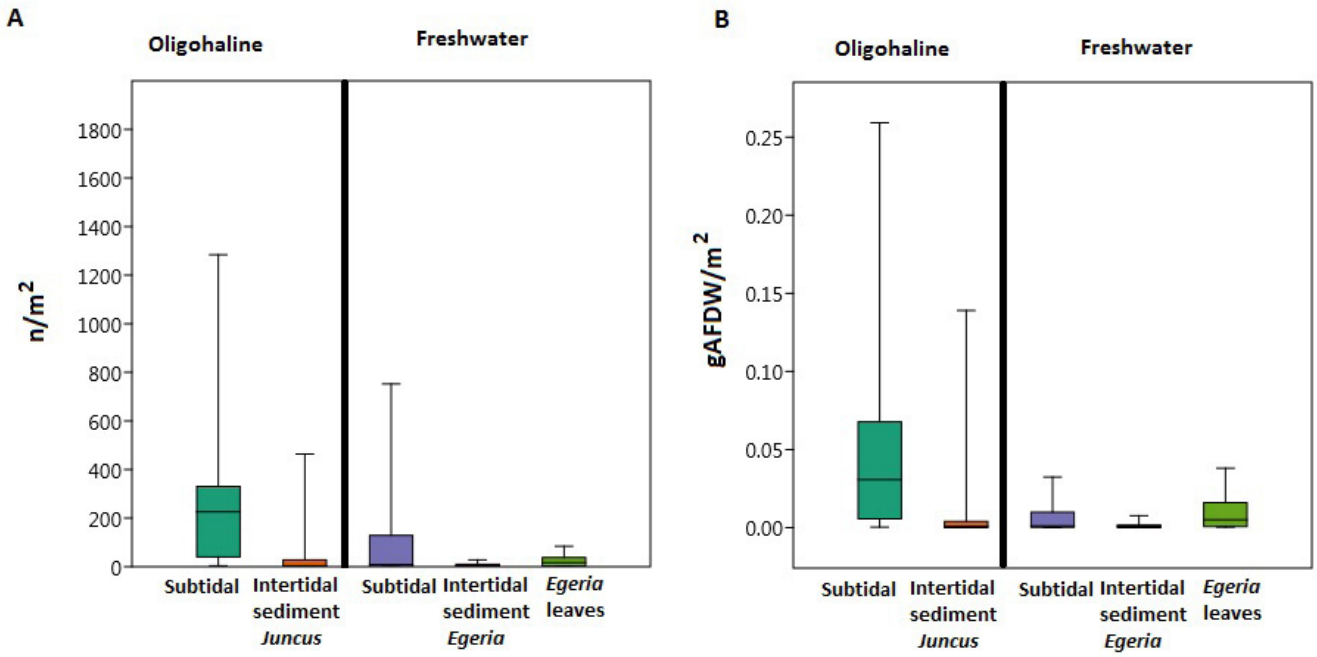

Figure 2- Mean *Gammarus chevreuxi* annual abundances (A) and biomasses (B) per site.
Figura 2- Abundancias anuales medias de *Gammarus chevreuxi* (A) y biomasas (B) por local de muestreo.

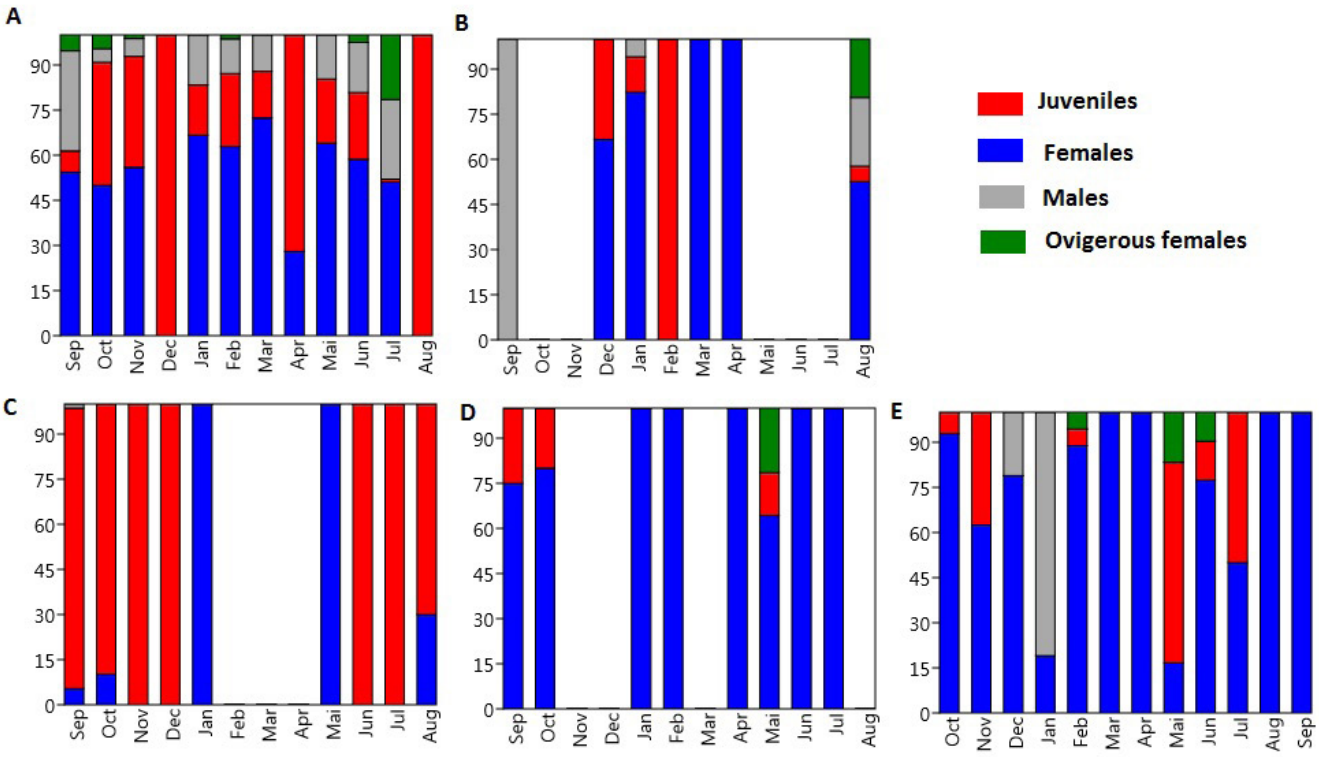

Figure 3- Monthly *Gammarus chevreuxi* class proportion (oligohaline subtidal (A); oligohaline intertidal sediment with *Juncus* spp. (B); freshwater subtidal (C); freshwater intertidal sediment with *Egeria densa* (D); freshwater *Egeria densa* macrophyte leaves (E)).

Figura 3- Proporción mensual de clases de *Gammarus chevreuxi* (submareal oligohalino (A); sedimento intermareal oligohalino con *Juncus* spp. (B); submareal de agua dulce (C); sedimento intermareal de agua dulce con *Egeria densa* (D); lechos de *Egeria densa* en agua dulce (E)).

3.2 *Corophium multisetosum*

The abundance and biomass of *Corophium multisetosum* were highest in oligohaline environments followed by the freshwater environment (Supp. file 1: Table S2). However, *Corophium multisetosum* was mostly absent in sediments with Egeria densa. In polyhaline environments, this species was less abundant (2 -4 individuals/m2 in intertidal sediments), with no specimens collected in subtidal sediments (Supp. file 1: Table S2). Overall abundance and biomass were higher in subtidal sediments (Figs. 4; Supp. file 2: Figs. S8, S9; Supp. file 1: Table S2). The two-way PERMANOVA analysis of abundance revealed that the habitat contributed the most to community variation (PERMANOVA: R2 = 0.40, F = 89.76, p<0.001). Seasonal variation (PERMANOVA: R2 = 0.07, F = 8.45, p<0.001) and the habitat/seasonal interaction (PERMANOVA: R2 = 0.04, F = 5.52, p<0.001) had small contributions. Biomass variation however seems to be highly dependent of all factors (habitat- PERMANOVA: R2 =0.22, F =40.71, p<0.001, season- PERMANOVA: R2 = 0.14, F = 11.75, p<0.001; interaction- PERMANOVA: R2 =0.33, F =5.53, p<0.001). Corophium multisetosum responded positively to salinity, whereas oxygen saturation and chlorophyll a concentration were negatively correlated with its abundance and biomass. The sex ratio was heavily skewed towards females (Fig. 5), which makes up approximately 90% of the total adult population. In oligohaline environments juveniles are present throughout the year, with peaks in abundance in autumn (Supp. file 2: Figs. S8, S10, S11, S12, S13). A decline in juveniles in freshwater environment was shown from winter to spring (Figs. 5; Supp. file 2: Figs. S14, S15). Peaks in the abundance of small individuals are mostly associated with subtidal sediments, whereas peaks in the intertidal sediment abundance during the summer are associated with an influx of large adult individuals (Fig. 6). In subtidal sediments, abundance and biomass were highest during autumn, whereas in intertidal sediments this peak occurred during summer (Supp. file 2: Fig. S8). Ovigerous females were found between late spring and autumn (Fig. 5) and were mostly absent in freshwater environments.

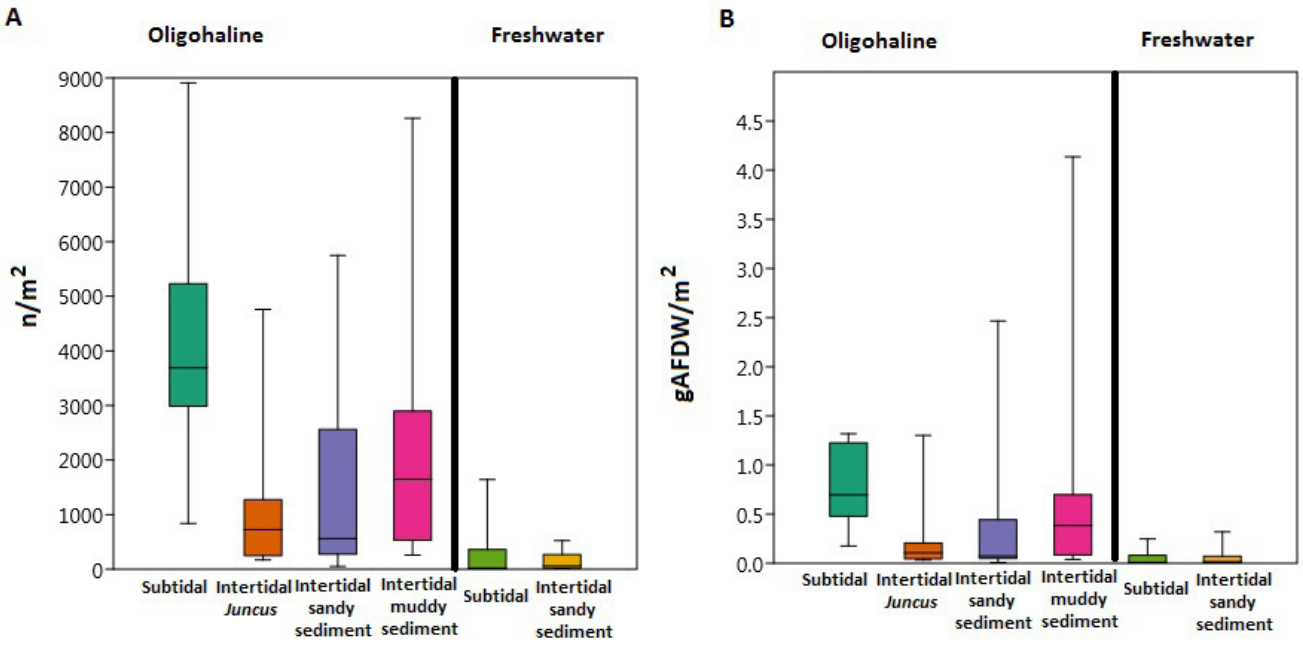

Figure 4- Mean *Corophium multisetosum* annual abundances (A) and biomasses (B) per site.
Figura 4- Abundancias anuales medias de *Corophium multisetosum* (A) y biomasas (B) por punto de muestreo.

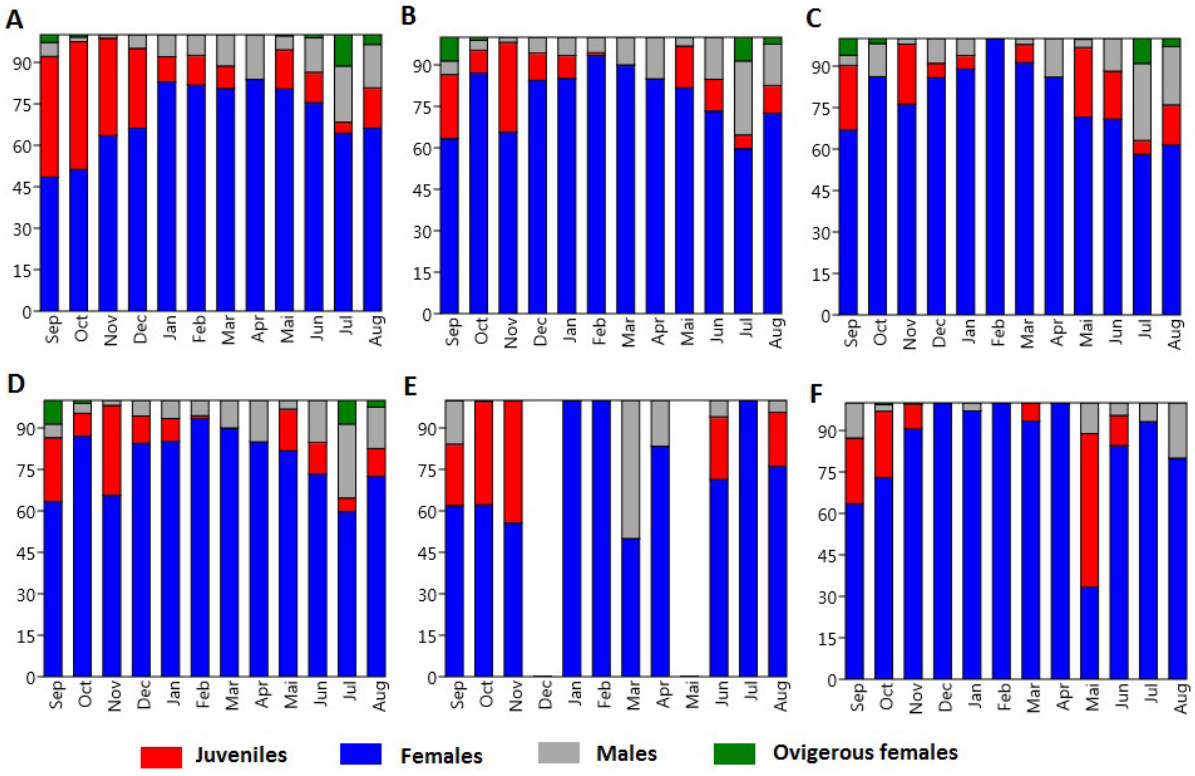

Figure 5- Monthly *Corophium multisetosum* class proportion (oligohaline subtidal (A); oligohaline intertidal sediment with *Juncus* spp. (B); oligohaline intertidal sand (C); oligohaline intertidal mud (D); freshwater subtidal (E); freshwater intertidal sand (F)).

Figura 5- Proporción mensual de clases de *Corophium multisetosum* (submareal oligohalino (A); sedimento intermareal oligohalino con *Juncus* spp. (B); arena intermareal oligohalina (C); lodo intermareal oligohalino (D); submareal de agua dulce (E); arena intermareal de agua dulce (F)).

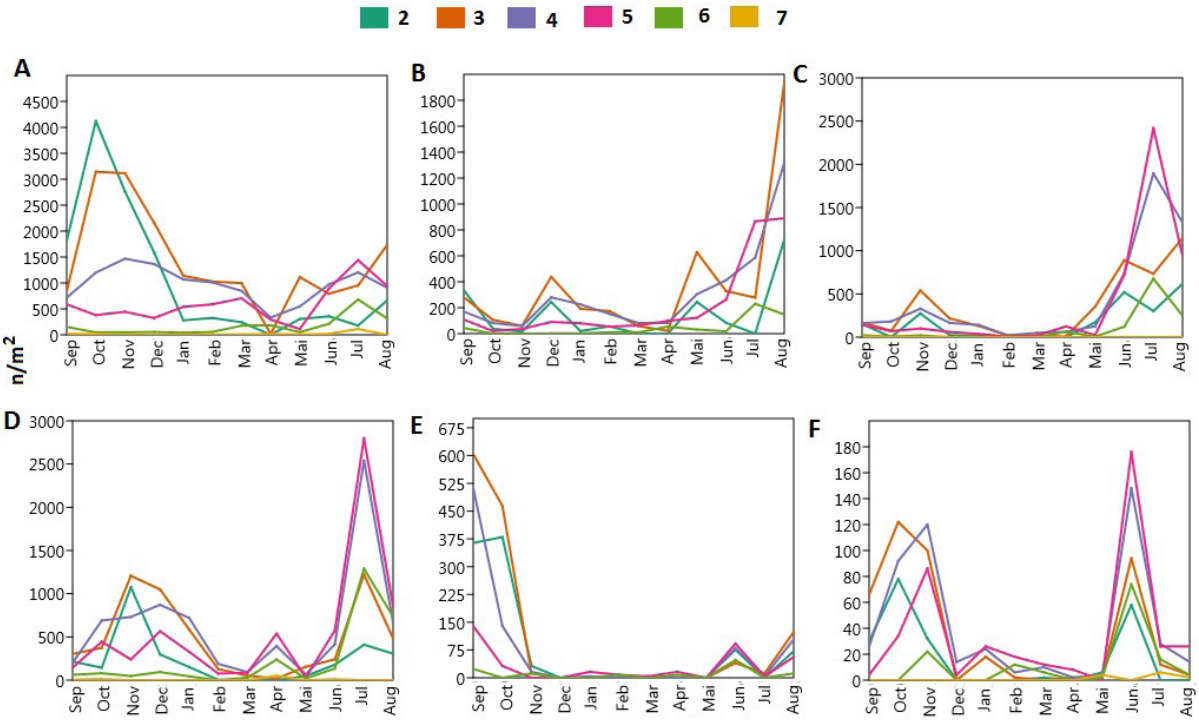

Figure 6- Monthly *Corophium multisetosum* abundances per size class (mm).

Figura 6- Abundancias mensuales de *Corophium multisetosum* por clase de tamaño (mm).

4. DISCUSSION

4.1 *Gammarus chevreuxi*

Gammarus chevreuxi is most abundant in the oligohaline section of the estuary and shows a clear preference for subtidal soft bottoms and intertidal sediments associated with macrophytes, although the reasons for this preference are still largely unknown. Peak abundance and biomass results in this section, occurring in July-August, do not coincide with the results obtained by Subida *et al*. (2005) in the Ria de Aveiro (approximately 170 km from the study area), where peak abundances were recorded in October and peak biomasses in February. In the lower estuary individuals were only recorded during months of high rainfall (March and April). As the period studied (2021/2022) was characterised by low rainfall and low flow rates, the migration to the lower estuary may have been affected. The mean annual abundance in the subtidal soft bottoms of the Minho River was 296 individuals/m^2 while in the Ria de Aveiro it has 16845 individuals/m^2 showing a large difference in density between these two sites. Autumn-winter populations represent the majority of the annual population in the Ria de Aveiro (Subida *et al*., 2005), whereas in the Minho River this trend shifts to spring-summer dominance. An important difference between these two sites is the presence of macrophytes in the subtidal sediments of the Ria de Aveiro, such as *Potamogeton* L. and *Myriophyllum* L. (Subida *et al*., 2005), whereas the subtidal soft bottoms of the Minho estuary are mostly bare, with a few patches of filamentous green algae and *Ulva* spp. that appear during the spring and summer months. In the Minho River the high availability of food resources, such as green algae, seems to provide the most favourable conditions for high density and biomass occurrence, leading to a shift in population demographics compared to those observed in Ria de Aveiro. These results suggest that *Gammarus chevreuxi* may be heavily dependent of vegetal substrates. Breeding takes place throughout the year, confirming the results obtained by Subida *et al*. (2005), with reproductive peaks occurring from October to November, similar to the Minho River populations, where these periods were observed between August and November. During autumn and winter, juveniles migrate upstream and constitute the majority of the freshwater population, confirming the results observed by Girisch *et al.* (1974) and Girisch & Dennert (1975). Peaks in adult mortality are observed after the reproductive period, with their disappearance from subtidal soft bottoms. Although adults disappear from these environments, summer and overwintering adults are still found in sediments with macrophytes. The sex ratio in the Minho River was strongly skewed towards females, while in the Ria de Aveiro was less pronounced. Female biased sex ratios under microsporidian parasitism were observed on *Gammarus duebeni* Lilljeborg, 1852 (Terry *et al*., 1998), with similar percentages of females being reported here. Furthermore, these same biased ratios were also observed on *Gammarus pulex* Linnaeus, 1758 due to estrogens environmental contamination (Watts *et al*., 2002)

4.2 *Corophium multisetosum*

Corophium multisetosum is most abundant in the middle section of the estuary and shows a preference for subtidal soft bottoms, although the reasons for this preference are still largely unknown. The lower abundances recorded in the lower estuary indicate that high salinity is a limiting factor for this species. In the middle section the results obtained regarding trends in abundance were consistent with those obtained in Ria de Aveiro by Cunha *et al.* (2000b), with peaks in abundance occurring during the autumn season. In Ria de Aveiro, biomass peaks were recorded from autumn to winter in Ria de Aveiro, whereas in the Minho River these peaks occurred from summer to autumn, indicating that adult reproductive upstream migration occurred early due to salinity pressure, possibly due to the low flow rates recorded during this period. The mean annual abundance in the subtidal soft bottom of the Minho River was 4229 individuals/m^2 while in the Ria de Aveiro it was 84 405 individuals/m^2, again showing a significant difference in density between these two sites. Overall, this species showed the same responses to environmental cues observed by Queiroga (1990) and Cunha *et al.* (2000b), responding positively to salinity in low water conditions and negatively to oxygen saturation and chlorophyll a concentrations. The negative correlation between vegetation biomass and *Corophium multisetosum* abundance found by Cunha *et al.* (2000b) was also observed in this study where oligohaline sediments with *Juncus* spp. had the lowest abundances in this environment and were mostly absent in *Egeria densa* sediments from the freshwater section. Breeding occurs throughout the year, confirming the results of Cunha *et al.* (2000b), with reproductive peaks occurring during the autumn. These results confirm that this is a cold-temperate

species with optimal reproductive conditions being favoured by colder temperatures, with autumn-winter populations representing the majority of the annual population. In late spring juveniles begin to migrate upstream where they mature, with peaks of juvenile recruitment to the upper estuary occurring in the autumn before returning to more saline environments in the winter. The absence of ovigerous females in freshwater environments indicates that most of the juvenile population is born in oligohaline/mesohaline environments, confirming the optimal breeding conditions at moderate temperatures (15-20°C) and salinities (2-18) observed by Cunha *et al.* (2000a). Large adults migrate to intertidal sediments from late spring to late summer, coinciding with the appearance of ovigerous females indicating that breeding takes place in intertidal environments. Similar to *Gammarus chevreuxi* the sex ratio in the Minho River was heavily skewed towards females, whereas in the Ria de Aveiro this was less pronounced. Female biased sex ratios were also observed for this species under microsporidian parasitism (Mautner *et al.*, 2007).

5. FINAL REMARKS

A summary of the traits from *Gammarus chevreuxi* and *Corophium multisetosum* is shown in Table 1. The nature and dynamics of the Minho River estuary appear to be less favourable for *Gammarus chevreuxi* and *Corophium multisetosum* populations than another estuary at similar latitude. Compared to the results obtained for the Ria de Aveiro, abundances are extremely low, with the main differences between these two systems being related to lower macrophyte coverage and chlorophyll a concentrations (Cunha *et al.*, 2000b; Subida *et al.*, 2005). Another important difference is the presence of the exotic clam *Corbicula fluminea* in the Minho River estuary, which has been shown to alter benthic invertebrate community dynamics (Ilarri *et al.*, 2014). Both amphipods have been shown to have migratory patterns within the salinity gradient as well as within the same environment, either between depth gradients or substrates. Juveniles tend to migrate upstream where they mature and adults migrate downstream where food is more readily available and conditions for reproduction are optimal. Salinity and temperature are the most relevant environmental cues for their distribution and reproduction within the salinity gradient, with both species having low tolerance for high salinity environments. The sex ratio is heavily skewed towards females however the observed ratio bias does not appear to be related to sampling bias, as several microhabitats were extensively sampled thorough the year, revealing no discernible male occupation patterns. These results prompt further studies into the causes of this phenomenon, such as verification of microsporidian contamination and intersex analysis. Furthermore, the effect of estrogenic compounds on these amphipod populations should also be considered as feminization of male fish was reported in this same estuary (Rodrigues *et al.*, 2006). In addition, the environmental cues for sex in *Corophium multisetosum* are still largely unknown. The inclusion of samples collected in mesohaline sediments and on the water column during flood tides may also provide further insight into the migratory patterns of this species.

Table 1- *Gammarus chevreuxi* and *Corophium multisetosum* traits at different systems.
Tabla 1- Características de *Gammarus chevreuxi* y *Corophium multisetosum* en diferentes sistemas.

	Gammarus chevreuxi	***Corophium multisetosum***
Habitat	Macrophytes; Soft bottoms (sand or mud); Rock bottoms (Subida *et al*,. 2005)	Soft bottoms (sand or mud) (Queiroga, 1990) Rock bottoms (Wijnhoven *et al.*, 2011)
Feeding behaviour	Grazer (Subida *et al.*, 2005)	Filter feeder; Deposit feeder (Møller & Riisgård, 2006)
Life cycle	Iteroparous biannual (Subida *et al.*, 2005)	Iteroparous biannual (Cunha *et al.*, 2000a)
Lifespan	6 months (Subida *et al.* 2005)	6 months (Cunha *et al.*, 2000a)
Mean annual abundance	Ria de Aveiro – 16845 individuals/m^2 (Subida *et al.*, 2005) River Minho – 296 individuals/m^2 (This study)	Ria de Aveiro – 84405 individuals/m^2 (Cunha *et al.*, 2000b) River Minho – 4229 individuals/m^2 (This study)
Reproductive peaks	Ria de Aveiro – October to November (Subida *et al.*, 2005) River Minho – August to November (This study)	Ria de Aveiro– Autumn (Cunha *et al.*, 2000b) River Minho – Autumn (This study)
Peak abundance	Ria de Aveiro – October (Subida *et al.*, 2005) River Minho – July to August (This study)	Ria de Aveiro – Autumn (Cunha *et al.*, 2000b) River Minho – Autumn (This study)
Upstream migration	River Dourduff – Late summer (Girisch & Dennert 1975) River Minho – Autumn–winter (This study)	Late spring – Autumn (This study)

Supplementary information ↑

Funding sources

Not applicable.

Supplementary material

Supp. file 1. Additional tables.
Supp. file 2. Additional figures.

Data availability

Not applicable.

Acknowledgements

Not applicable.

Authorship contribution statement

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Nuno Gomes. The first draft of the manuscript was written by Nuno Gomes and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Competing interests

The authors of this article declare that they have no financial, professional or personal conflicts of interest that could have inappropriately influenced this work.

Statement on the use of Artificial Intelligence

Not applicable.

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