

Modelling the variation in larval dispersal of estuarine and coastal ghost shrimp: *Upogebia* congeners in the Gulf of Cadiz

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ABSTRACT: *Upogebia pusilla* and *U. deltaura* are 2 common ghost shrimp species occurring in estuaries and over the shelves of European coasts, respectively. The adults have a great impact on benthic habitats and communities, as they depend on sandy and muddy substrates to construct long burrows that provide shelter and appropriate conditions for reproduction and feeding. Their planktonic larval phase lasts around 3 wk and consists of 4 zoeal stages and a decapodid that must settle in the benthos before recruiting to adult populations. *In situ* data were obtained from CTD casts and plankton hauls during an oceanographic survey that took place along the southern Portuguese coast in August 2010. All zoeal stages and decapodids of both species were found distributed over the shelf not exceeding 30 km from the coastline. A modelling approach was used to explain the differences in dispersal of these *Upogebia* congeners inhabiting different habitats of the same geographic area and exposed to similar oceanographic conditions. Their vertical distribution, oceanic circulation and the points of larval release were considered. A different dispersal strategy, influenced by natal origin and vertical behaviour, was evident for each species. The presence of decapodid stages close to substrates suitable for settlement where adult populations occur, especially for *U. deltaura*, suggests a good probability of successful settlement. Dispersal patterns observed for the 2 species and the agreement between field observations and model simulations indicate that these species are good models for other coastal invertebrates that reproduce in summer and have short larval development.

KEY WORDS: Decapoda · *Upogebia pusilla* · *Upogebia deltaura* · Gulf of Cadiz · Larval transport · Modelling · ROMS · Ichthyop

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INTRODUCTION

In their life cycle, marine benthic decapods have a pelagic larval phase which, being exposed to the oceanographic conditions, can be dispersed away from parental habitats. Larval behaviour, especially the type and frequency of vertical migrations, plays an important role in their survival rate (e.g. Morgan et al. 2009) and in the success of their settlement and

recruitment processes, which are of great importance for the sustainability of both populations and the habitats they use.

Species of the genus *Upogebia* represent some of the most abundant decapods inhabiting intertidal and subtidal sediments of coastal areas all over the world. In particular, *U. pusilla* and *U. deltaura* are 2 common ghost shrimp species that occur in the Mediterranean Sea and eastern Atlantic Ocean (from Nor-

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way to Mauritania), and also in Portuguese estuaries and shelf seas (Zariquiey-Álvarez 1968, dos Santos & Paula 2003). Adult populations have a great influence on bottom sediments, as well as on the benthic communities (e.g. substrate aeration and increase of organic decomposition; Pinn et al. 1999), constructing long systems of burrows in which they live and that offer them protection from predators and appropriate conditions for reproduction and feeding (Li et al. 2008). On the other hand, the use of *Upogebia* species as live bait has grown and, consequently, several populations around the world have suffered decreases in their abundance (Hodgson et al. 2000, Faleiro & Narciso 2009).

Upogebia species undergo a short-duration larval phase that lasts around 3 wk and consists of 4 zoeas and a decapodid (Faleiro et al. 2012). However, when environmental conditions are adverse, a tendency to surpass the last zoeal stage is observed, with larvae moulting directly to the decapodid stage (Paula et al. 2001). The decapodid stage must settle in the benthos before recruiting to adult populations, and for successful settlement, it is of great importance to rapidly find the appropriate type of substrate. *U. pusilla* depends on soft muddy sediments while *U. deltaura* can also occur on coarser sand and gravel given their relatively larger size as adults (Kevrekidis et al. 1997, Hall-Spencer & Atkinson 1999). It is thought that the last zoeal and decapodid stages may play an important role in the selection of substrate for settlement, responding to characteristics such as the content of organic matter, as has been observed in *Callichirus* species, which are also ghost shrimps with a burrowing behaviour (Strasser & Felder 1999a,b).

Upogebia pusilla is a typical estuarine species occurring in shallow waters, while *U. deltaura* is a coastal species occurring on the shelf mainly between depths of 20 and 40 m (Zariquiey-Álvarez 1968, Paula 1993). Given their distribution and burrow construction behaviour, these organisms are difficult to sample. As a result, the abundance of the adult population is commonly underestimated and limited information is available, especially for *U. deltaura*.

The first zoeal stage (Z1) of *Upogebia pusilla* is thought to be exported outside the estuaries to complete development in nearshore ocean waters. Confirming this scenario, Paula (1993) found only Z1 larvae at the lower reaches of the Mira estuary (Portugal), and Landeira et al. (2012) observed all zoeal stages in ocean waters off the Canary Islands. Also, Faleiro et al. (2012) found a maximum survival for *U. pusilla* larvae at salinity values of 35 and tempera-

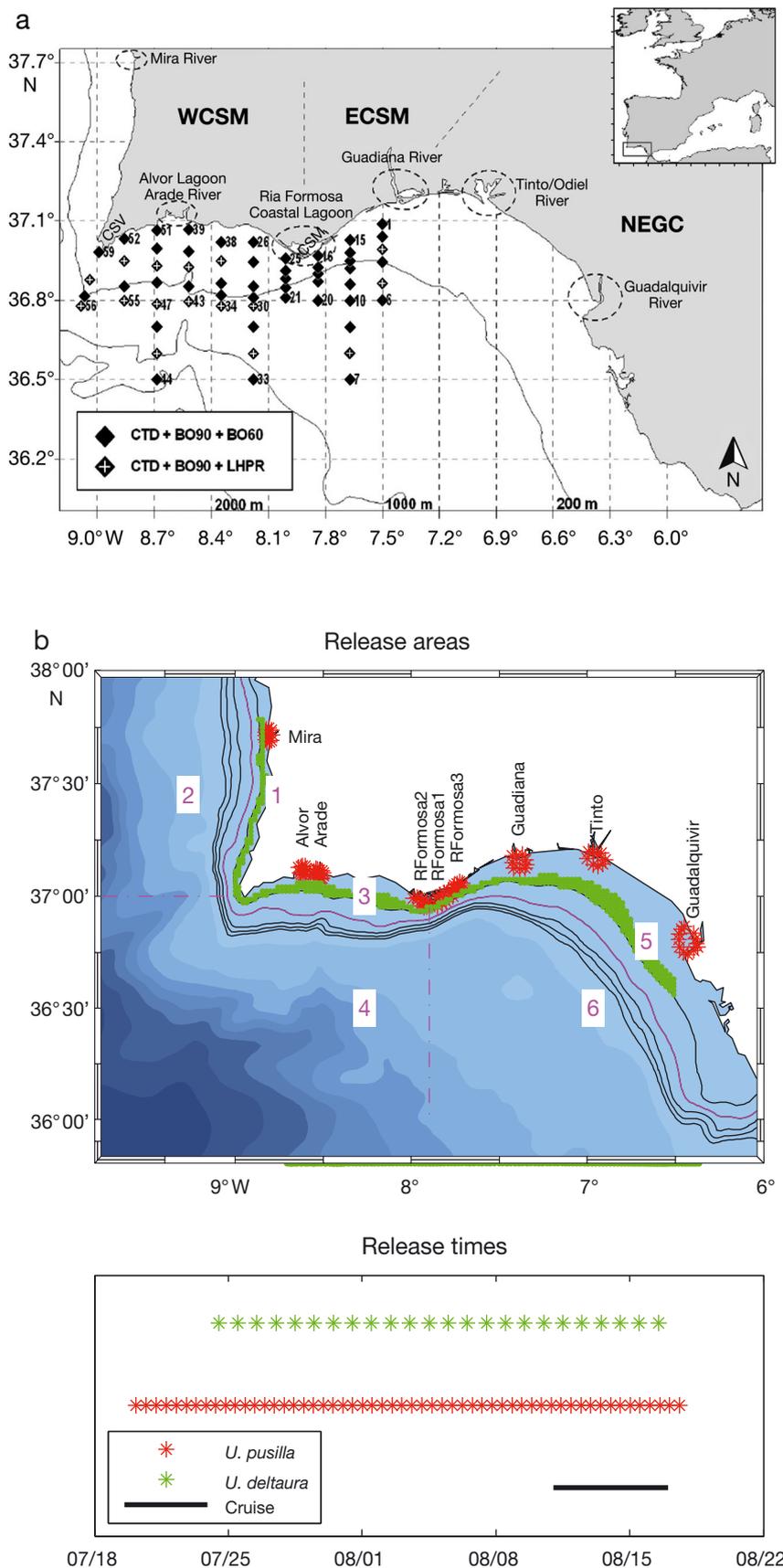
tures between 23 and 28°C, with salinity being the limiting factor and temperature influencing the duration of the larval stages. The occurrence of vertical migrations in *Upogebia* larvae has been reported in several studies, either according to the period of day/night (diel vertical migrations, DVM; Russell 1931, Paula 1993) or associated with tidal currents (Dworschak 1988). After completing their larval development in nearshore waters, decapodids of species whose adults depend on estuarine or sheltered areas return to these parental habitats, as demonstrated for *U. africana* (Wooldridge & Loubser 1996). Candisani et al. (2001) detected juvenile burrows of *U. noronhensis* always associated with the burrows of adults, verifying this idea of a return to adult habitats.

For the Gulf of Cadiz and particularly for the Portuguese coast, the few studies available about *Upogebia* larvae do not address the influence of oceanographic features on their dispersal and recruitment to parental populations. Therefore, we analysed the mechanisms involved in the dispersal range and retention of *U. pusilla* and *U. deltaura* larvae. In view of the fact that these congeners inhabit different habitats in the same geographic area and under similar oceanographic conditions, their vertical migration behaviour, substrate selection for settlement and the oceanic circulation in the area were taken into consideration. Our hypothesis was that the origin of larvae and their vertical position in the water column influence their dispersal range and retention in shelf waters. We thus expected that *U. pusilla*, the estuarine species, would be more effectively retained than *U. deltaura*, which was expected to be subjected to a larger dispersal range. A larval dispersal modelling experiment was conducted to verify this hypothesis, and the results were extensively compared to *in situ* data.

MATERIALS AND METHODS

Relevant aspects of the oceanography of the study area

The south coast of Portugal (Algarve) is located on the northwestern part of the Gulf of Cadiz between Cape S. Vicente and the Guadiana River (Fig. 1a). At Cape S. Vicente (37°N), the Portuguese coast changes from a meridional to a zonal orientation, separating a coast extremely exposed to northerly winds and almost permanent upwelling in summer from a relatively sheltered shelf to the south. The



shelf is narrow (~25 km wide) west of Cape Sta. Maria and begins progressively widening to the east (~40 km, on the Spanish side). West of Cape Sta. Maria, the freshwater inputs from the Arade River and Alvor lagoon/River are weak, contrasting with the important runoff from Guadiana, Tinto, Odiel and Guadalquivir Rivers east of Cape Sta. Maria. Another important feature of the coastline is the Ria Formosa coastal lagoon (Fig. 1a).

The surface shelf circulation of the northern Gulf of Cadiz is described as 2 cyclonic circulation cells separated by Cape Sta. Maria (Garcia-Lafuente et al. 2006). Over the upper slope/shelf break, the Gulf of Cadiz Slope Current flows eastward and is an important component of the Atlantic inflow into the Mediterranean Sea (e.g. Peliz et al. 2009a). During summer, under the influence of northerly winds, the western Portuguese coast is characterized by coastal upwelling conditions (e.g. Relvas et al. 2007), but the east-west orientation of the southern coast does not favour coastal upwelling, since westerly winds tend to be weak, intermittent and less frequent (Relvas & Barton 2002). Nevertheless, the shelf is influenced by the eastward spreading of the cold waters that upwelled either at Cape S. Vicente or farther north (e.g. Relvas et

Fig. 1. (a) Southwestern coast of Portugal (Algarve region) and Gulf of Cadiz showing the sampling sites, the nets used at each station (BO90: Bongo 90 cm; BO60: Bongo 60 cm; LHPR: Longhurst Hardy Plankton Recorder), the main coastal features (CSV: Cape S. Vicente; CSM: Cape Sta. Maria) and the sub-areas considered (WCSM: west of Cape Sta. Maria; ECSM: east of Cape Sta. Maria; NEGC: northeastern Gulf of Cadiz). The larval release locations are also indicated by ellipses. (b) Release areas and timeline of particle release experiments relative to the cruise dates. Colours represent species (red: *Upogebia pusilla*; green: *U. deltaura*). Numbers 1–6 represent each of the 6 areas considered in the estimation of proportions presented in Table 1, separated by Cape S. Vicente, Cape Sta. Maria and the 100 m isobaths

al. 2007). Furthermore, the Gulf of Cadiz Slope Current intensifies this eastward spreading of upwelling waters over the shelf break/slope along the northern Gulf of Cadiz. During upwelling relaxation and under easterly winds (Levantine episodes), a near-shore westward countercurrent advects warm and salty waters over the inner shelf along the northern Gulf of Cadiz, curls around Cape S. Vicente and flows northward along the southwestern Portuguese coast (Relvas & Barton 2005, Garcia-Lafuente et al. 2006, Teles-Machado et al. 2007). Under strong easterly wind conditions, this coastal counter flow connects the inner shelves of the 2 areas separated by Cape Sta. Maria. All of these circulation features are surface intensified, decaying significantly in the upper 100 to 150 m. Due to the presence of the Mediterranean water circulating along the slope, an intensification of the currents for depths below 300 m is observed (e.g. Peliz et al. 2009a).

Fieldwork

Sampling took place during a research cruise aboard RV 'Noruega' from 11 to 17 August 2010 along the northwestern Gulf of Cadiz between the Guadiana estuary and Cape S. Vicente (Fig. 1a). This survey was carried out within the scope of the multidisciplinary project MedEx (MARIN-ERA/MAR/0002/2008; www.marinera-medex.eu).

In total, 59 stations were sampled between the longitudes 7° 30.0' W and 9° 05.2' and the latitudes corresponding to the 30 m isobath and 36° 30.0' N. A CTD SBE 911p fitted with a Chelsea Aqua Tracka III Fluorometer was used to collect data on temperature, salinity and chlorophyll *a* with depth.

Zooplankton sampling was performed at all of the 59 stations using a Longhurst Hardy Plankton Recorder (LHPR) sampler, and/or Bongo nets (60 and 90 cm mouth aperture diameter). The LHPR was used to analyse the vertical distribution of the larvae, while the Bongo 60 was employed to sample mainly zoeal stages and the Bongo 90 to capture the last larval stages (megalopae/decapodids). All nets were equipped with flowmeters. The LHPR was used at 16 stations with a 280 µm mesh net and filtering gauze. Samples were collected during descent at 25 m depth intervals, the net being towed at 4 knots on oblique hauls from the surface until near bottom or around 400 m at the deeper stations. At stations where the LHPR was not used, a Bongo net with a 60 cm diameter aperture and a mesh size of 335 µm was employed. At all stations, a Bongo net with a 90 cm

diameter aperture and mesh size of 750 µm was used. Both Bongo nets were towed on depth-integrated double oblique hauls at ±2 knots from the surface to 10 m above the bottom or until 200 m depth at deeper stations.

Sample processing

The plankton samples were preserved in 4% borax-buffered formaldehyde prepared using seawater. After the determination of biovolume by the displacement method (Hagen 2000), the samples were sorted and analysed for *Upogebia* larval identification and staging. Samples with more than 400 larvae were sub-sampled using a Folsom splitter. Zoeal stages were identified to the species level following the identification keys of dos Santos & González-Gordillo (2004) and confirmed with dos Santos & Paula (2003) and Webb (1919). The decapodid stage showed great morphological variation within the 2 species, which prevented their separation to species level; therefore, they were analysed jointly for both species. The numbers of larvae were standardised to individuals per 10 m³ using filtered volume values, and these abundances were plotted on maps of spatial distribution by geolocation to analyse the horizontal distribution of the larvae. Vertical distribution was also investigated using LHPR-stratified data with 25 m depth resolution intervals and combining all day and night stations. A Kruskal-Wallis statistical analysis was performed to evaluate whether the differences between the vertical distributions of each species were statistically significant.

Modelling

Peliz et al. (2013) developed a long-term, high-resolution simulation for the Gulf of Cadiz-Alboran Sea sub-basin. This simulation was extended for the year 2010 to cover the observed period. The model consists of a Regional Ocean Modelling System (ROMS; Shchepetkin & McWilliams 2005) application on a ~2 km grid and 32 vertical levels, with 200/5 seconds for the baroclinic/barotropic mode. A 3D order advection scheme is used for momentum and tracers; the vertical mixing is parameterized using a K-Profile Parameterization (KPP) scheme. For the sake of conciseness, we will not provide a detailed description of the model configuration and validation and refer the reader to Peliz et al. (2013), to the series of papers referred to therein, especially Peliz et al. (2007b,

2009a,b), and to Oliveira et al. (2009). The present configuration is oriented to shelf slope mesoscale processes and for that reason tides were not included. Only the Guadalquivir River was simulated in the model because most of the rivers have a very small outflow in summer months (with the exception of the Guadalquivir) and due to the absence of river outflow data from the study period. For the 2010 summer period, the model was forced with realistic satellite-derived winds (advanced scatterometer; Figa-Saldaña et al. 2002) re-gridded into the model grid together with the ERA-Interim heat fluxes. The model 3D temperature, salinity and velocity fields were stored with a 4 h frequency for later use with offline Lagrangian particle tracking experiments.

The Lagrangian experiments were conducted with Ichthyop (Lett et al. 2008). Ichthyop is a particle tracking based model which includes a set of parameterizations designed for plankton dispersal and recruitment simulations running over 3D realistic ocean models. Using same ocean model outputs, a set of experiments was designed with Ichthyop, varying parameters like release time, location and number of particles, DVM modes and horizontal diffusivity (following Peliz et al. 2007a). To increase the realism of the experiments, the simulations were conducted in such a way that the final particle distributions could be evaluated at the same times and locations as the observations, taking into account the zoeal space density distribution (per station and vertical stratum). As for the initialization of particles, they were based on *a priori* knowledge of the species' life cycles and also on larval and adult distributions in the study area. There are, however, considerable gaps in the knowledge, and some sensible assumptions had to be made. The model-observation comparisons should thus be interpreted with caution.

The dispersal experiments started approximately 1 mo before the end of the survey period (see Fig. 1b for the release areas and the timeline of the experiments). Releases of particles were done instantaneously every day for *Upogebia deltaura* and every tidal cycle for *U. pusilla* during the simulation period considered (around 30 d). Since no mortality was added to the model, the lifetime of each particle ends with the simulation period, when it leaves the model domain or when it reaches the coast. Particle connectivity was estimated between 6 areas separated by Cape S. Vicente, Cape Sta. Maria and the 100 m isobath (see Fig. 1b). The connectivity values show the percentage of particles that are emitted in a given area and arrive at a target area (high values corre-

spond to retention in the release area or dispersal to other areas).

For *Upogebia pusilla* simulations, the following settings were used: (1) Larval release was done 3 h after each flood (Paula, 1993), within a small area (~10 km radius) off all rivers and lagoons (Fig. 1b) since this species is an estuarine dweller. The amount of emitted particles was uniform for all release points/times (1000 individuals). (2) Based on the vertical distributions obtained from LHPR samples, different groups of particles were forced to conduct different DVMs (0–25, 15–45, 25–60 and 45–75 m), with the particles floating at the surface during the night period (22:00–04:00 h; dos Santos et al. 2008). (3) For each zoeal stage lifetime, the following intervals were adopted: ZI, <3 d; ZII, 3–8 d; ZIII, 8–16 d; and ZIV, 16–21 d (Faleiro et al. 2012).

In *Upogebia deltaura* experiments, the following settings were used: (1) A homogeneous release of particles along the shelf between the 30 and 50 m isobaths from the area adjacent to the estuary of the Mira River (southwestern Portuguese coast) to the vicinity of the Guadalquivir River mouth because of the potential occupation of shelf habitats by adults and the analysis of sediment type distribution charts; releases occurred at 00:00 h (Dworschak 1988). (2) Based on the vertical distributions obtained from LHPR samples, a single DVM was used with particles floating at 10 m during the night (22:00–4:00 h; dos Santos et al. 2008) and at 40 m during the remaining time. (3) For each zoeal stage duration we used: ZI, <2 d; ZII, 3–9 d; ZIII, 9–14 d; and ZIV, 14–18 d. It is important to highlight that due to the lack of studies on the larval duration for *U. deltaura*, the larval duration chosen took into account the studies of Paula (1993) and Paula et al. (2001). These studies suggest a tendency for coastal larvae of decapod species to reduce larval duration and even surpass the last stages when environmental conditions are inappropriate. Estuarine larvae can adapt more easily to temperature and salinity variations, especially in the first stage (Paula 1993). Also, several tests were performed considering different durations for each stage to understand its influence on larval distribution.

RESULTS

Oceanographic conditions during the cruise

Northerly wind conditions (upwelling favourable) off the southwestern coast of Portugal prevailed during the weeks before (since 20 July 2010) and

during the cruise (Fig. 2). The main exceptions were observed during the period of 26–28 July, 7–9 August and 14–15 August 2010, when the wind relaxed and changed to easterlies. The northerlies favour the development of upwelling off Cape S. Vicente and the recirculation of the equatorward upwelling jet into the northwestern part of the Gulf of Cadiz. In the Gulf of Cadiz, especially west of Cape Sta. Maria ($\sim 8^\circ$ W), the wind speed and direction were variable. Important events of easterlies could be observed just before the cruise (between 7 and 9 August 2010; Fig. 2a), and by the middle of it (14–15 August 2010; Fig. 2c), the latter with the occurrence of lower-intensity winds. The occurrences of easterlies and relaxation of the northerlies on the southwestern coast allowed the intrusion to the west of the warm innershelf countercurrent just prior to the cruise (Fig. 3d). Coastal upwelling adjacent to Cape S. Vicente and the innershelf countercurrent

are clearly seen in the distributions of the sea surface temperature (SST) from the ROMS model (Fig. 3a,e,g) which agree well with the SST distribution obtained during the cruise (not shown).

Distribution of *Upogebia pusilla* zoeal stages

All larval stages of *U. pusilla* were found in the samples. The first zoeal stage (ZI) remains near the coast (Fig. 4a), with greater abundances being located in the nearshore area adjacent to Alvor lagoon/Arade River, Ria Formosa coastal lagoon and Guadiana River. The abundances of the second zoeal stage (ZII) are higher than for ZI but similar through the sampling stations, with the horizontal distribution remaining mainly over the shelf but reaching areas off Ria Formosa coastal lagoon where the shelf is deeper and very narrow (Fig. 4a). The third (ZIII) and fourth (ZIV) zoeal stages

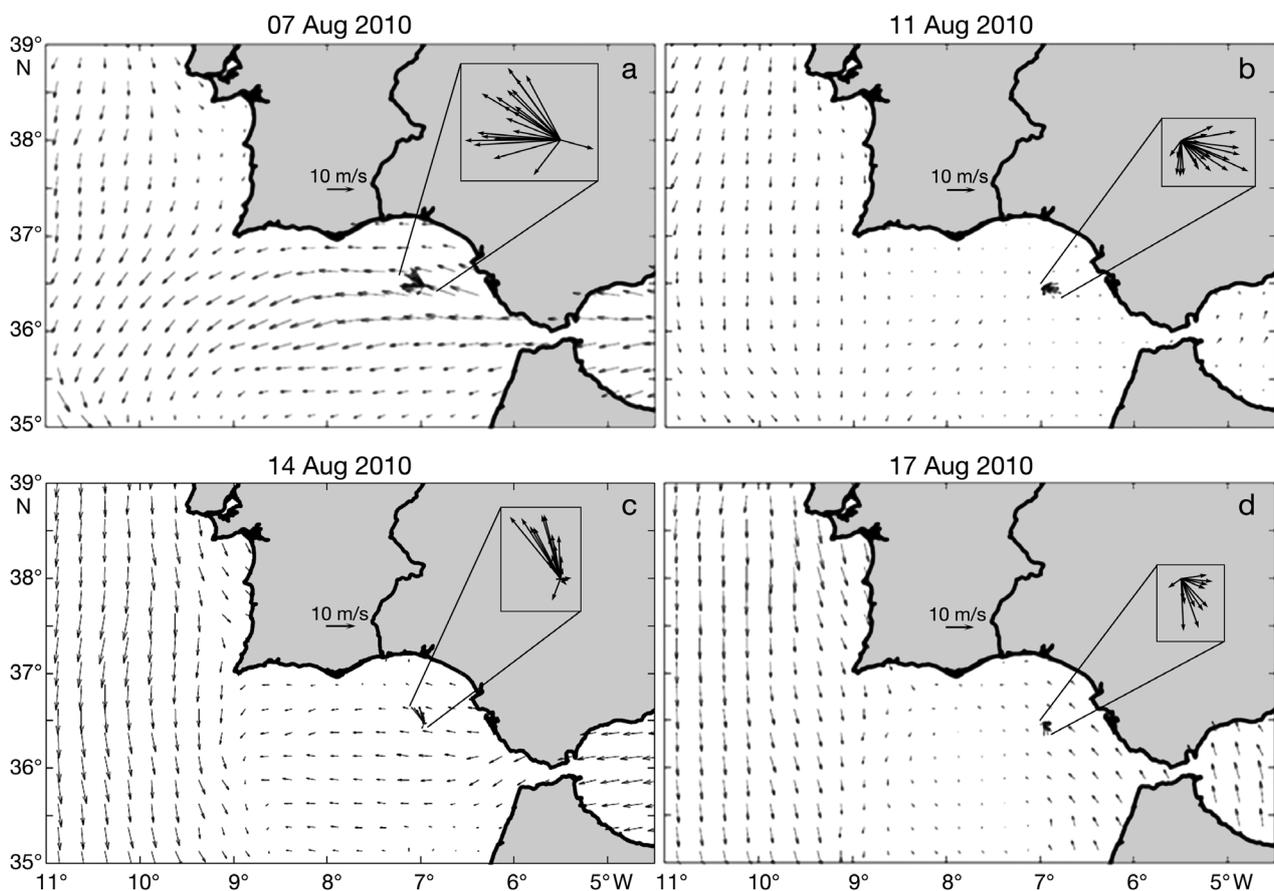


Fig. 2. Wind speed and directions over the Gulf of Cadiz measured by the MetOp satellite on (a) 7 August (before the cruise), (b) 11 August (cruise beginning), (c) 14 August (middle of the cruise) and (d) 17 August 2010 (cruise end). Inset shows a zoom of the vectors at the Gulf of Cadiz buoy of Puertos del Estado ($36^\circ 49' \text{ N}$; $6^\circ 97' \text{ W}$); 24 vectors show the hourly averages of each day. Arrow lengths correspond to velocity

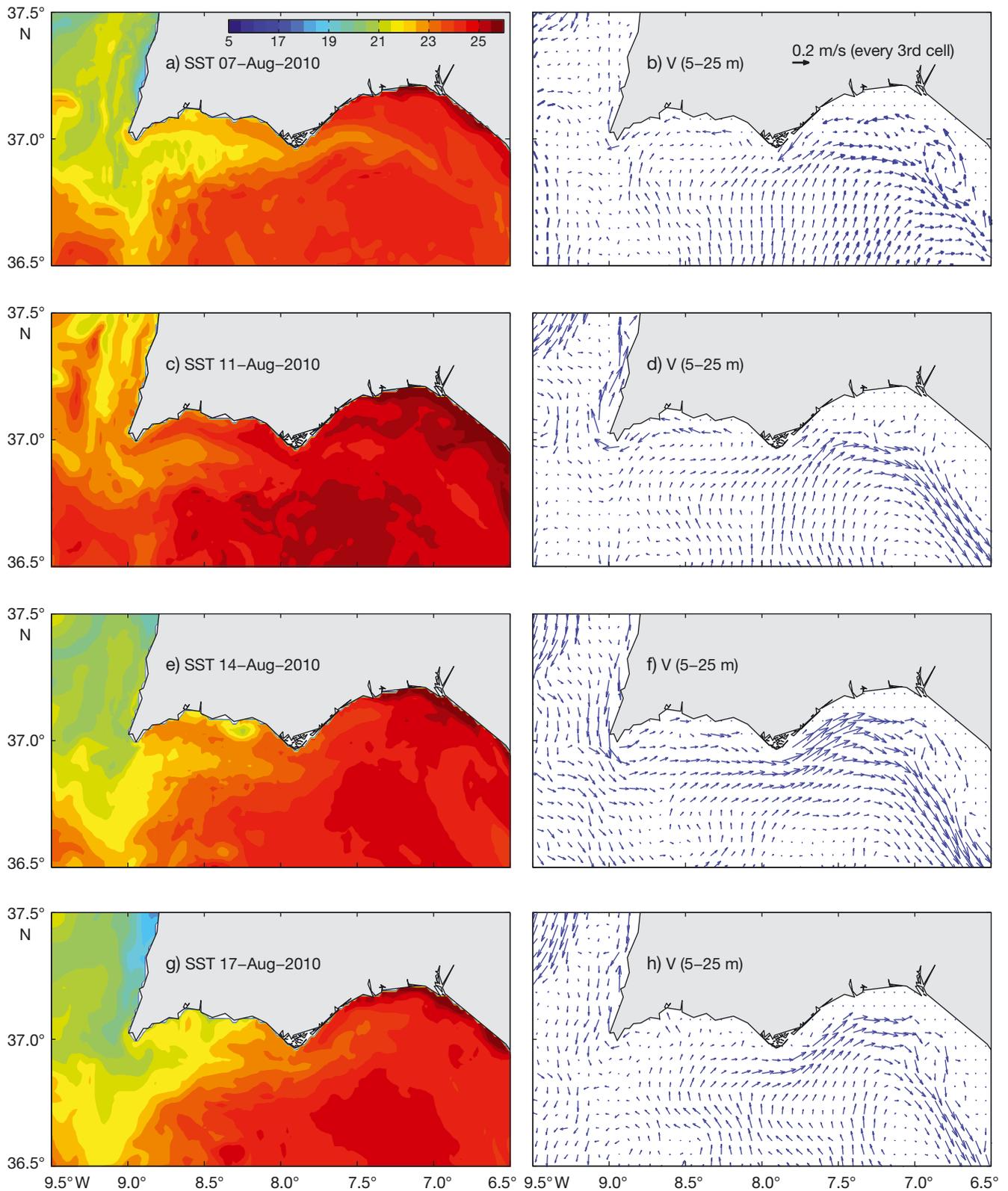


Fig. 3. Sea surface temperature (SST, °C) distribution on (a) 7 August (before the cruise), (c) 11 August (cruise beginning), (e) 14 August (middle of the cruise) and (g) 17 August 2010 (cruise end). Surface current speed (at 5–25 m depth) and directions over the Gulf of Cadiz from ROMS model outputs (see description in 'Materials and methods') on (b) 7 August, (d) 11 August, (f) 14 August and (h) 17 August 2010. The vector scale (black arrow) corresponds to 0.2 m s^{-1} . Arrow lengths correspond to velocity

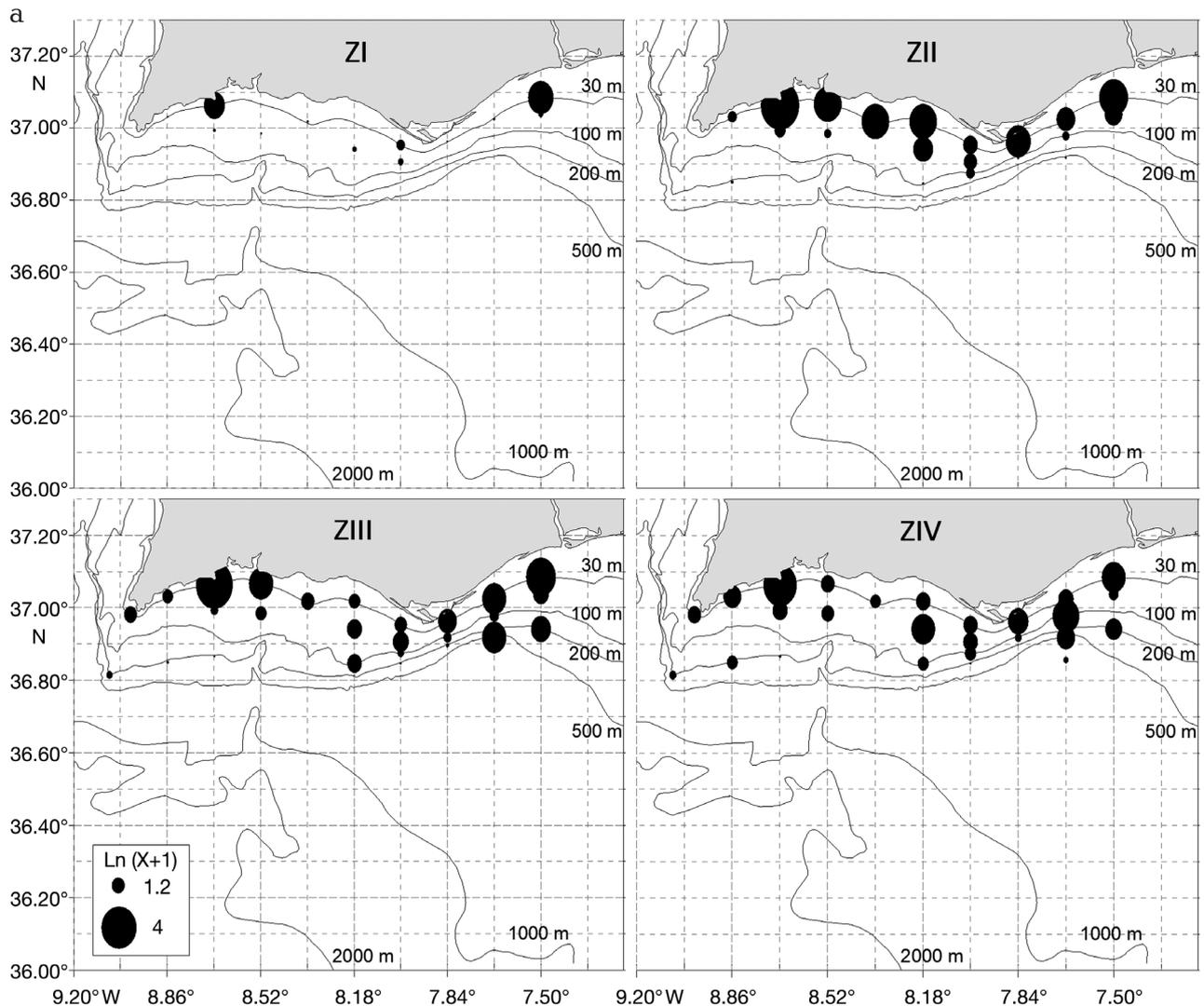


Fig. 4. *Upogebia pusilla* and *U. deltaura*. Abundances ($\ln [x + 1]$ where $x = \text{ind. } 10 \text{ m}^{-3}$) of all zoal stages (ZI–ZIV) for (a) *U. pusilla* and (b) *U. deltaura*, collected with the Bongo 60 net

undergo larger dispersion, and a considerable number of individuals are observed at offshore locations off Cape Sta. Maria and Cape S. Vicente, unlike the first stages. Still, the bulk of their abundance is located over the shelf (Fig. 4a). These older stages are also more abundant within an innershelf band of about 30 km with highly populated patches off the main coastal lagoons and estuaries, namely the Alvor lagoon, Arade River, Guadiana River and Ria Formosa coastal lagoon, which are the potential areas for larval release in the northwestern Gulf of Cadiz. Another interesting observation is that older stages occur in a much wider area than the younger ones, indicating that larvae of this species present an increasingly wider distribution over the shelf throughout their development.

With regard to their vertical distribution, the zoal stages occur from the surface down to 150 m depth, although a larger share of individuals is observed between 25 and 50 m (Fig. 5a). ZI was not found in these samples due to their nearshore distribution; conversely, only ZIII and ZIV were found at deeper levels from 75 to 150 m (Fig. 5a).

The relative abundances and spatial distribution obtained with model simulations (Fig. 6a,b; see also Figs. S1 and S2 in Supplement 1 at www.int-res.com/articles/suppl/m492p153_supp/) agree well with the general distribution of the first zoal stage for this species. This occurs at places close to the coast, mainly in areas with estuarine influence. Model larvae, however, tended to concentrate to the east of the river mouths, whereas the observed concentrations

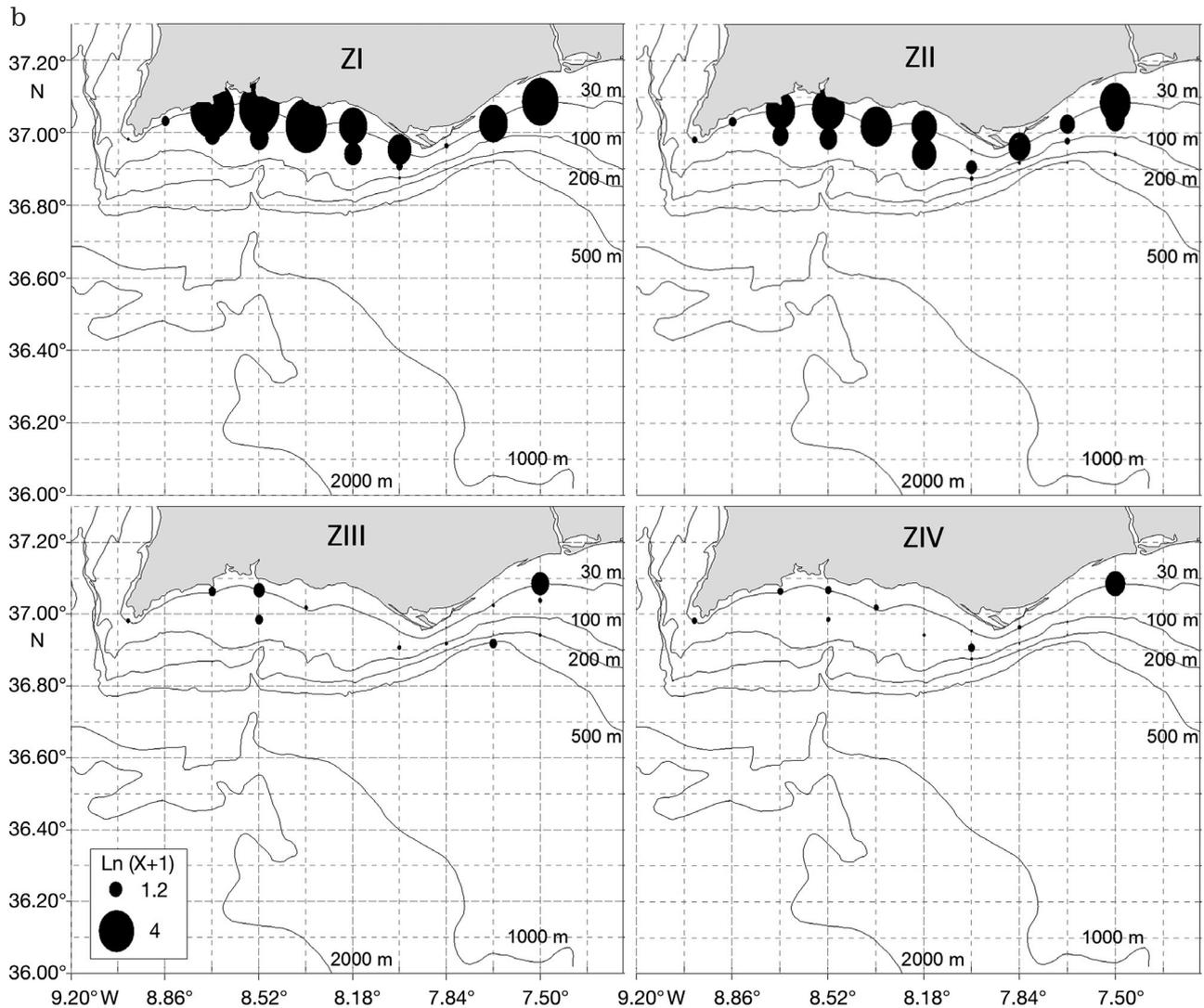


Fig. 4 (continued)

tended toward the west (this small difference has to do with the misrepresentation of the rivers in the model and will be discussed later). When compared with the observations, the distribution of older stages is also well represented by the model. The good agreement between *in situ* data and model results allows for other inferences on the distribution patterns of larvae where no observations are available, namely, the estuaries located along the Spanish coast of the Gulf of Cadiz (Tinto, Odiel and Guadalquivir Rivers) and farther north on the southwestern Portuguese coast (Mira River).

The simulation (Table 1a, Fig. 7a; see also Animation 1 in Supplement 2 at www.int-res.com/articles/suppl/m492p153_supp/) shows that larvae released from the Alvor lagoon, Arade River and Ria Formosa

lagoon systems are exposed to higher dispersion (around 10% more) than larvae released in north-eastern Gulf of Cadiz (NEGC) estuaries (e.g. Tinto/Odiel and Guadalquivir Rivers), which present a higher retention (99.4%). Furthermore, model simulations suggest that there is a greater contribution of larvae (9.6%) that originated from northwestern Gulf of Cadiz estuaries to the NEGC shelf (Spanish coast; areas A5 and A6 in Table 1a) than the opposite (0.21%; areas A3 and A4 in Table 1a).

Larvae released on the southwestern coast of Portugal (at the Mira estuary) have a reduced contribution (less than 0.5%) to the larval pool of the area west of Cape Sta. Maria (WCSM) as the majority remain in the area (92.7%) or are dispersed to offshore waters (Table 1a). On Cape S.

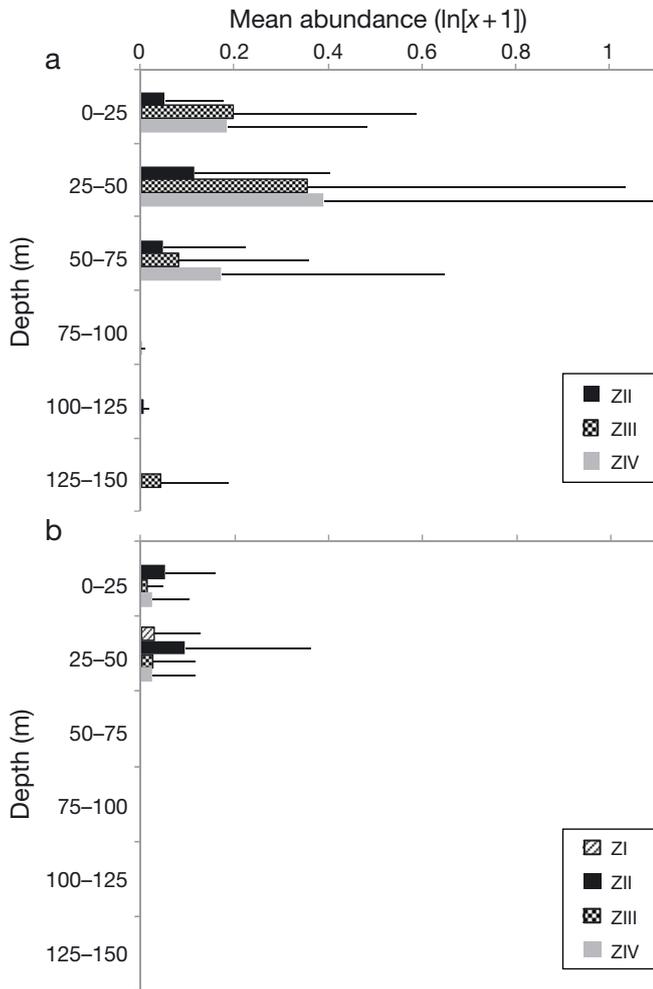


Fig. 5. *Upogebia pusilla* and *U. deltaura*. Mean \pm SD of vertical abundances ($\ln [x + 1]$ where $x = \text{ind. } 10 \text{ m}^{-3}$) of all zoeal stages (ZI–ZIV) of (a) *U. pusilla* and (b) *U. deltaura*

Vicente, the offshore loss of larvae also seems to be significant.

Distribution of *Upogebia deltaura* zoeal stages

All zoeal stages of *U. deltaura* were found in the samples and in relatively high numbers, with ZI being more abundant than the same stage of *U. pusilla* (Fig. 4b). This stage remains mainly over the shelf in areas where depth is less than 100 m; the highest abundances occur along the 30 m isobath in similar values along the coast (Fig. 4b). ZII remains mainly over the shelf with abundances similar to those found for the first stage (Fig. 4b). However, ZIII and ZIV are absent from more stations and present a notable decrease in abundances compared to previous stages (Fig. 4b). This large decrease in abun-

dance is not verified for ZIII and ZIV stages of *U. pusilla* larvae that occur widely on the shelf. Higher numbers of *U. deltaura* later stages were observed in the eastern stations located between the Guadiana River and Ria Formosa coastal lagoon area (hereafter called ECSM).

Regarding their vertical distribution, all zoeal stages of *Upogebia deltaura* appeared to be limited to the upper 50 m of the water column (Fig. 5b). In fact, the differences in the vertical distribution are only statistically significant for ZIII and ZIV stages of both species ($p = 0.012$ and 0.006 , respectively).

Again, the model agrees with the observed larval distributions (Figs. 4b, 6c,d; Figs. S3 & S4 in Supplement 1). However, older stages (ZIII and ZIV) in the model seem to be overestimated, as their decrease in terms of abundance is not as evident as observed in the *in situ* data, particularly in the adjacent region west of the Ria Formosa coastal lagoon. In the simulations, larvae are absent from offshore stations and remain over the shelf, with the exception of the Cape S. Vicente region (Fig. 6c,d; Figs. S3 & S4 in Supplement 1). Model simulation also suggests large retention at ECSM and NEGC and high offshore larval transport from the WCSM area, especially near Cape S. Vicente (Table 1b, Fig. 7b; Animation 2 in Supplement 2).

Once again, the contribution of larvae that originated on the southwest coast (over the shelf adjacent to the Mira River and up to Cape S. Vicente) is not significant for the northwestern Gulf of Cadiz area

Table 1. *Upogebia pusilla* and *U. deltaura*. Connectivity between shelf areas (A1–A6) separated by Cape S. Vicente, Cape Sta. Maria and the 100 m isobath (see Fig. 1b), according to the percentage of particles emitted in one area that arrive at another or remain retained, for (a) *U. pusilla* and (b) *U. deltaura*. Areas where no particles were emitted are indicated by an X

(a)	A1	A2	A3	A4	A5	A6
A1	92.7157	6.8558	0.0434	0.3742	0	0.0108
A2	X	X	X	X	X	X
A3	0.1097	0.0084	88.9373	1.3529	7.9011	1.6905
A4	X	X	X	X	X	X
A5	0	0	0.2102	0.0006	99.3731	0.4161
A6	X	X	X	X	X	X
(b)	A1	A2	A3	A4	A5	A6
A1	82.1100	14.5130	2.3584	1.0187	0	0
A2	X	X	X	X	X	X
A3	3.4051	0.0909	80.5482	7.4116	7.0130	1.5313
A4	X	X	X	X	X	X
A5	0	0	0.9423	0	93.2419	5.8158
A6	X	X	X	X	X	X

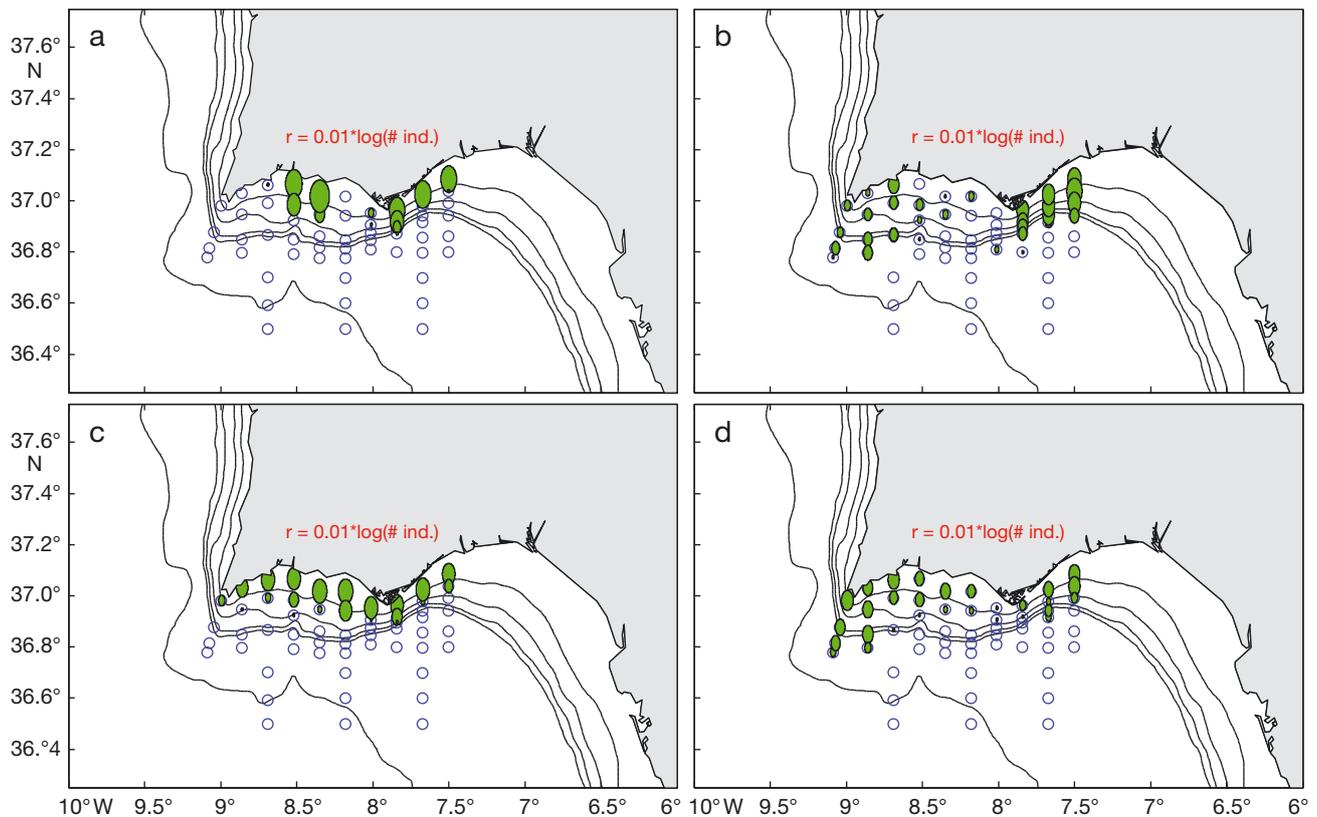


Fig. 6. *Upogebia pusilla* and *U. deltaura*. Relative abundances (represented by the size of the green bubbles) for the first and fourth zoeal stages of (a,b) *U. pusilla* larvae and (c,d) *U. deltaura* larvae obtained in the model simulations (see complete data for each species in Figs. S1 & S3, respectively, in Supplement 1). Open circles represent the sampling points in the survey

(only 3.4%; Table 1b). Larval dispersal to offshore waters on the southwest coast of Portugal (Mira) and on the south coast at Cape S. Vicente is significant and certainly helps to explain the observed lower abundances registered for the older zoeal stages in the cruise data.

Distribution of *Upogebia* decapodid stage

Decapodids are present at most of the sampling stations, mainly over the shelf and hardly appearing in offshore oceanic waters (>200 m bottom depths; Fig. 8). The highest abundance occurs in the area adjacent to the Ria Formosa coastal lagoon over bottom depths shallower than 50 m, and above (*U. deltaura*) or near (*U. pusilla*) potential settlement grounds.

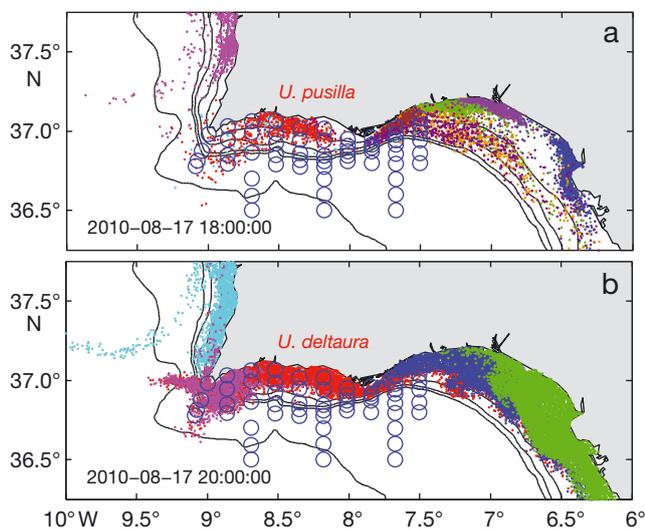


Fig. 7. *Upogebia pusilla* and *U. deltaura*. Snapshot showing the dispersal simulated by the model for (a) *U. pusilla* and (b) *U. deltaura* larvae at the end of the oceanographic survey (see Animations 1 & 2 in Supplement 2, respectively). Open circles represent the sampling points in the survey. Coloured points represent the different groups of larvae released (for *U. pusilla*, pink: Mira river, light blue: Alvor lagoon, red: Arade River, dark purple: west Ria Formosa, orange: east Ria Formosa lagoon, green: Guadiana River, light purple: Odiel/Tinto Rivers, dark blue: Guadalquivir river; for *U. deltaura*, light blue: west coast of Portugal, pink: Cape S. Vicente area, red: area between Cape S. Vicente and Cape Sta. Maria, dark blue: area between Cape Sta. Maria and Odiel/Tinto Rivers, green: area between Odiel/Tinto Rivers and Cadiz Bay)

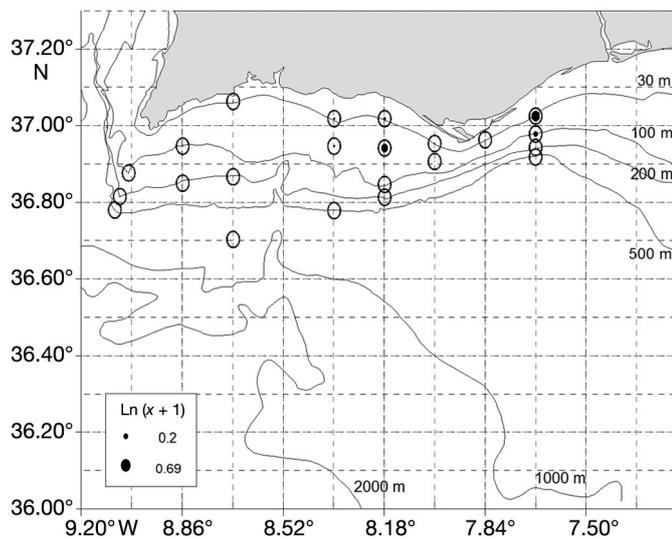


Fig. 8. *Upogebia* spp. Abundances ($\ln[x + 1]$ where $x = \text{ind. } 10 \text{ m}^{-3}$) of decapodid stages for *Upogebia* species (filled ovals). All stations where decapodids occurred are also highlighted (O)

DISCUSSION

Upogebia pusilla belongs to the group of species that, despite being estuarine, have larvae that are exported to the adjacent ocean waters to complete their development (Dworschak 1988, Faleiro et al. 2012). The last larval stage, a decapodid, must then return to the estuarine parental grounds (Wooldridge & Loubser 1996). The observed abundances of the first zoeal stage (ZI) agree with a larval release originating in estuarine and coastal lagoons of the WCSM and ECSM areas. These ZI locations are also predicted by the model simulations considering the advection conditions, before and at the time of plankton sampling, and the potential natal release points. The natal origin of larvae is actually one of the most important factors to take into account in studies of population dynamics and connectivity (Cowen et al. 2007, Pineda et al. 2007). The fact that tidal currents and river runoff were not included in the model explains the difference between observed and model distributions off the estuaries, namely the occurrence of larvae east (west) of the estuaries in the model (observations). In the absence of significant opposing winds, larvae being emitted from the estuaries should be deflected to the west in association with the river plume dynamics. It is clear by the increasing occurrences from ZI to ZIV that the complete larval development of this species takes place mainly at shelf waters where larvae present a high probability of successful settlement.

The observed abundances of *Upogebia deltaura* larval stages also suggest that they develop over the shelf, as do *U. pusilla*. However, a wider distribution of *U. deltaura* ZI along the inner shelf is observed, a consequence of the distribution and abundance expected for their adults. For *U. pusilla*, this wider distribution over the shelf was only observed for ZII and older stages. Although the available literature suggests a similar reproductive period for both species, from spring to summer (Zariquiey-Álvarez 1968, Paula 1993), distinct periods of larval release in nature could contribute to these contrasting scenarios. In fact, given the short duration of the sampling, the spatial patterns observed do not allow any clear conclusion on the temporal extension of the release, and a delay may exist between *U. pusilla* and *U. deltaura* release peaks. Thus, the sampling period could have captured larvae of both species at different stages of their development and dispersal due to different larval release peaks. Rhythms of larval release have been studied for decapod species (e.g. Forward 1987, Paula 1989) and revealed the night period, associated with high tides and semilunar phases, as the most important for estuarine and coastal species. Therefore, species would release the larvae when conditions are the most appropriate for exportation or dispersal, although synchrony of larval release may also enhance larval survival (Paula 1989).

Nevertheless, according to the estuarine/coastal habitats of each species, model simulations suggest different distributions in the considered period, evident in the number of particles retained in waters shallower than 100 m: *Upogebia pusilla* larvae occur closer to the coast, concentrated near their release locations especially in the northeastern Gulf of Cadiz; *U. deltaura* larvae present a greater cross-shore dispersion and particles disperse much more in relation to their natal sites. Larval release points and the vertical distribution will determine the type of currents which larvae will be exposed to. However, the more scattered natal sites of *U. deltaura* induce larger uncertainties in the dispersion patterns.

In the WCSM area, *Upogebia* larvae experience highly variable but usually slower alongshore shelf currents that contrast with those observed over the slope (the quasi-steady Gulf of Cadiz Slope Current: Peliz et al. 2009a). This creates a boundary zone and limits the dispersal pattern to a preferential larval drift along the coast (e.g. Largier 2003). In northern California (USA), for example, this boundary region

reaches 10 km from shore (Kaplan & Largier 2006). The back and forth transport according to the horizontal circulation over the shelf coupled with the up and down movement of DVM that reduces the net effect of the cross-shore currents favours the retention of larvae nearshore. A similar process is observed for decapod larvae off the Aveiro coastal lagoon system (northwestern Portuguese coast) that develop on the inner shelf where they undergo a much smaller cross-shelf transport than the along-shore one (Marta-Almeida et al. 2006, Peliz et al. 2007a, dos Santos et al. 2008).

However, a more distant occurrence from the coast than *Upogebia pusilla* and the limitation to surface layers (first 50 m) may expose the early stages of *U. deltaura* to higher cross-shore dispersal, as suggested by the simulations. The disappearance of the last zoeal stages from the survey area suggests that larvae of *U. deltaura* could have been swept off the shelf. On the other hand, a different period of larval release in relation to *U. pusilla* could mean that the last stages did not have enough time to develop. Higher dispersal rates will probably have more impact on the recruitment of *U. pusilla* than of *U. deltaura* since the potential settlement sites for decapodids of the latter species are available throughout the shelf (see discussion below). Some recruitment at ECSM and NEGC would also be possible as model simulations and observed decreasing abundances for ZIII and ZIV stages suggest.

For a similar larval release period, we believe that the differences in abundance of the last 2 zoeal stages of *Upogebia deltaura* and *U. pusilla* could be mainly a consequence of a greater dispersal of the former. Since larvae of both species are morphologically similar and differ in small details (dos Santos & González-Gordillo 2004), we believe they should be exposed to similar predation and feeding rates. Therefore these factors would not play significant roles in the observed differences.

The differences in abundance of ZIII and ZIV between species are not apparent in the model results. This inconsistency is probably related to the spatial uniformity of the release defined for *Upogebia deltaura* larvae in the model. This option is based on the availability of suitable substrates throughout the shelf. However, this does not necessarily mean that *U. deltaura* adult populations are equally distributed along the coast. According to Morgan & Fisher (2010), species tend to explore areas with stable circulation patterns to utilize retention or dispersal pathways. Likewise, *U. deltaura* adults may avoid areas where the ocean circulation is stronger or

unstable, such as, for example, the Cape S. Vicente area. Nevertheless, given the lack of specific information on adult distribution, preference was given to a uniform distribution in the model's larval release.

Intermittent upwelling events also have an important influence in the WCSM region, contrary to what occurs at the ECSM and NEGC. This fact may lead to a relatively greater offshore dispersion and to the establishment of barriers to alongshore transport in some cases/zones. Landeira et al. (2012) detected a strong relationship between the distribution of *Upogebia pusilla* larvae and the location of the upwelling front and filaments for all zoeal stages. They concluded that the persistence of these wind-driven events was responsible for the offshore occurrence of some larvae. In our case, the larval dispersal observed off Cape S. Vicente and the Mira River adjacent areas in the model simulations can also be related to these events. As do most headlands, Cape S. Vicente represents an obstacle to shelf currents and constitutes a preferential site of coastal upwelling enhancement interrupting the alongshore transport and leading to offshore loss of larvae and recruitment variability (Kaplan & Largier 2006). Slope circulation may act as a barrier preventing a large dispersal to offshore waters by leading larvae into cyclonic currents and back to nearshore areas (Bilton et al. 2002). In addition, it is proposed that the nearshore distribution of decapod larvae parallel to the coast would reflect the current features of the inner shelf associated with wind-driven events (dos Santos et al. 2008). For relatively more offshore waters, the same kind of distribution was observed for cirripede cyprids (dos Santos et al. 2007).

In the ECSM and NEGC areas, alongshore currents and the cyclonic cell circulation seem to favour a higher retention than in WCSM. Cape Sta. Maria also acts as an obstacle to the dispersion of larvae. However, in periods of easterly winds, some connection between both sides can occur, although to a lesser extent in the ECSM-WCSM direction than in the opposite direction (WCSM to ECSM) (Table 1). It is important to note that the continental shelf is very narrow in front of the Ria Formosa coastal lagoon, inducing a local acceleration of the along-shelf flow, since the cross-shelf movements are constrained (Sánchez-Arcilla & Simpson 2002). Thus, larvae with an origin in this coastal lagoon will be more exposed to the outer shelf currents off Cape Sta. Maria and will be transported back and forth to the western and eastern region, depending on the circulation in the area. Areas with a wider shelf, as in the case of NEGC, present a high cross-

shore transport that can result in a great retention potential when associated with eddy circulation (e.g. dos Santos & Peliz 2005).

For coastal invertebrates, Shanks (2009) stated that larval behaviour and the occurrence in deeper layers of the water column where currents are less energetic promotes retention in coastal waters by limiting their transport. The occurrence of *Upogebia pusilla* larvae in deeper layers than *U. deltaura*, especially the older stages, may help them to remain nearshore and exposed to slower rates of dispersal than in surface layers (first 5 to 10 m). Later stages of *U. deltaura* larvae can disperse more and suffer a higher loss from coastal areas to offshore. DVM has to be considered an important factor that influences the vertical position of larvae and promotes shelf retention (e.g. Santos et al. 2006, dos Santos et al. 2007). On the Portuguese shelf, modelling studies confirm DVM as a driving factor of retention near the release sites of larvae (Marta-Almeida et al. 2006, Peliz et al. 2007a).

Larval duration constitutes another critical factor for dispersal (Shanks 2009). Spending less time in plankton will assure retention near natal sites and the avoidance of being transported to unsuitable areas. Species with a long larval phase have a tendency to be highly dispersed, reaching greater distances from the coast (Cowen et al. 2007, Shanks 2009), as in the case of *Panulirus* larvae (Phillips 1981).

For each species, the decapodid stage must face different situations when searching for suitable settlement grounds near the adult habitats. Depending on sheltered areas, *Upogebia pusilla* has to reinvade coastal and estuarine areas while *U. deltaura* can find a suitable settlement place on the shelf. Based on sediment type distribution charts, finding a suitable settlement site will not be a problem for *U. deltaura* since sandy and muddy substrates are available all over the Gulf of Cadiz shelf. However, several cues can trigger the settlement of decapod larvae (dos Santos et al. 2004). Nevertheless, we believe that even *U. pusilla* decapodids will be able to find appropriate settlement grounds, as they were present in stations closer to the coast.

Although the model simulations do not include all factors controlling larval distribution, and despite the uncertainty in many of the initial conditions, the simulations seem to be robust and represent the main features of the observed distributions. Thus, these models could be applied to larvae of other marine invertebrate organisms inhabiting coastal areas with short plankton larval duration and used to predict their dispersal. Finally, this work can be considered

as a reference point for future studies, namely with regard to scenarios of climatic change and their effect on larval dispersal and recruitment of coastal benthic populations.

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