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ORIGINAL ARTICLE

Mesoscale advection of *Upogebia pusilla* larvae through an upwelling filament in the Canaries Coastal Transition Zone (CTZ)

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Abstract Larval transport has a strong influence on marine populations and ecosystem function. Traditional hypotheses establish that larvae of coastal species are swept offshore during strong upwelling periods producing low recruitment rates; however, recent studies have demonstrated that this hypothesis is not supported by larval distribution data. The present study examines the influence of upwelling filaments on larval advection and wastage. During August 1993, the transport of *Upogebia pusilla* was analysed in relation to an offshore filament off Northwest Africa. This mesoscale structure was generated by a trapped, quasi-permanent cyclonic eddy located between the Canary Islands and the African shelf and extended 150 km westward into the oligotrophic open ocean waters. The horizontal distribution depicted by *U. pusilla* larvae was strongly influenced by the oceanographic features of the Canaries Coastal Transition Zone (CTZ). Specifically, the larvae were closely associated with upwelling front and filament position, showing that these neritic larvae can be advected 10–100s of kilometres offshore through the filament. However, the low larval densities observed in the samples suggest that many larvae might remain close to the coast, thus avoiding seaward transport. This implies that filaments probably do not significantly affect the recruitment success of intertidal invertebrates such us *U. pusilla* in upwelling systems.

Keywords *Upogebia pusilla* · Larval transport · Upwelling filament · Canaries CTZ

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Introduction

Ocean currents have long been recognized as a major factor in larval transport, one that plays an important role in population and ecosystem dynamics (Roughgarden et al. 1988; Shanks 1995). Transport processes during the larval phase are critical, since retentive and dispersive phenomena could determine larval fate. This is of special interest in recruitment limited regions, such as upwelling systems, where dispersive mechanisms exert a strong influence over the nearshore communities (Ebert and Russell 1988; Connolly and Roughgarden 1998; Menge et al. 2003). According to these authors, the larvae behave as "passive" particles that may therefore be swept offshore during upwelling periods and shoreward during downwelling periods. The upwelling circulation could transport larvae far from shore preventing them from settlement, thereby resulting in a high loss of potential recruits. Consequently, these authors suggested that the strength and temporal variation of upwelling might explain the variations in recruitment in these particular ecosystems. However, recent studies have pointed out that the hypothesis of rapid larval transport during upwelling/downwelling may be incorrect (Shanks et al. 2003; Shanks and Brink 2005; Shanks and Shearman 2009; Morgan et al. 2009a, b; Morgan and Fisher 2010). In fact, these studies found no consistent differences in the cross-shelf distribution of

invertebrate larvae during upwelling and downwelling periods. This suggests that larval retention may be more widespread in upwelling regions than is widely believed and, therefore, recruitment variations must be explained in other ways.

Upwelling filaments are seasonally important components of the circulation throughout the eastern boundary upwelling regions and can transport zooplankton from the continental shelf to the open ocean (Barton et al. 1998). The causes of these filaments are varied. They can be formed by (1) the convergence of different water masses near the coast giving rise to unidirectional flow in water tongues towards the ocean ending with "T" or mushroom shapes (Marín et al. 2003), (2) an eddy slowly moving parallel to the coast (Barton et al. 1998) or (3) an unstable coastal jet, generating meanders and displacing upwelled waters towards the ocean (Strub et al. 1991).

The Moroccan subregion presents year-round upwelling, characterized by high levels of mesoscale oceanographic activity, such as eddies and filaments, during summer (Arístegui et al. 2009). Near Cape Juby and Cape Bojador, the Canary Islands archipelago introduces mesoscale variability in the form of downstream vortices (Arístegui et al. 1994) that frequently entrain upwelled waters (Barton et al. 2004). Moreover, the combination of weak stratification, wide continental shelf and persistent favourable winds can aid the formation of filament structures near those capes (Marchesiello and Estrade 2009). These filaments usually are less than 20 km wide and 200 m in depth in the Canaries Coastal Transition Zone (CTZ) and exert influence over the nano- and picoplankton (Baltar et al. 2009), phytoplankton (Navarro-Pérez and Barton 1998) and mesozooplankton communities (Hernández-León et al. 2002). Several case studies demonstrate strong offshore advection of eggs and fish larvae in the Moroccan upwelling area (Rodríguez et al. 1999, 2004; Bécognée et al. 2009). Despite the basic knowledge of plankton–filament interaction, there are no studies on the current-related transport of invertebrate larvae.

The main goal of this paper is to analyse the offshore distribution pattern of the mud shrimp *Upogebia pusilla* larvae in relation to a filament structure during a strong upwelling period off NW Africa. We hypothesize that these larvae may be transported to the open ocean, as was previously observed for fish larvae during the same cruise (Rodríguez et al. 1999). A second objective is to provide new insights into larval dynamics to improve understanding of the fluctuations in recruitment in upwelling areas. The growing demand of *U. pusilla* as live bait by recreational anglers has led to a decline in natural populations (Faleiro and Narciso 2009). However, management of these harvested bait stocks is rendered difficult by lack of information about the biology of this species from shallow soft bottoms. The present study is a contribution to the knowledge of the African populations of this mud shrimp and will be useful to the future establishment of protocols for fishery management.

Materials and Methods

In order to study the larval transport through the upwelling filament, a grid of stations, arranged in six transects separated by 30 km and parallel to the African coast, was

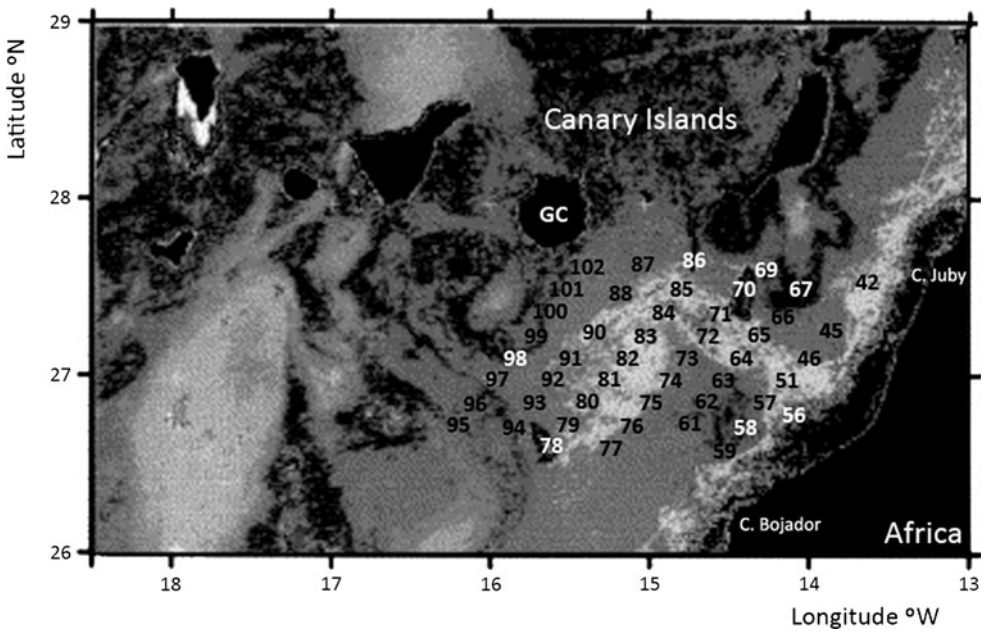

Fig. 1 Sea surface temperature image of 4 August 1993. *Numbers* indicate the positions of the stations. *G* Gran Canaria island

sampled in the Canaries CTZ (Fig. 1). The station closest to shore was located 20 km off the coast, while the furthest was 180 km offshore. The cruise took place between 9 and 16 August 1993, on board the *RV Hesperides*. Zooplankton was sampled at 47 stations using a WP-2 net, 200 μm mesh size (Fig. 1). The net was towed vertically from 200 m depth to the surface (or from 10 m above the bottom in shallower stations), and the samples were fixed in 5% buffered formalin. Vertical profiles of temperature, conductivity and fluorescence were obtained at every station using a SeaBird CTD, while an acoustic Doppler current profiler (ADCP) was used to measure the vertical profile of currents throughout the cruise.

In the laboratory, the larvae of *Upogebia pusilla* were sorted, counted and standardized to number per 100 m^3. The species identification and developmental stage were determined according to dos Santos and Paula (2003). Sampling was conducted around the clock, and consequently, diel vertical migrations could obscure the horizontal pattern observed (Queiroga and Blanton 2005). Therefore, one-way ANOVA was performed to compare the difference in larval abundance between day samples (station numbers: 42, 56–59, 65–67, 74–78, 82–86, 90–94, 99–102) and night samples (station numbers: 46, 45, 51, 61–64, 69–73, 80, 81, 88, 95, 96, 98).

Hierarchal clustering was performed to identify environmental assemblages among stations in the studied area. The cluster classification was represented in terms of the Euclidean distance dissimilarity matrix with the normalized oceanographic data (temperature and salinity) at (1) the sea surface, (2) 25 m and (3) 50 m depth (Clarke and Warwick 2001). These multivariate analyses were carried out using the PRIMER v6 statistical package (Clarke and Gorley 2006). To test whether the abundance of *U. pusilla* larvae was similar across the studied area, we used a one-way ANOVA that incorporated as factors the groups of stations detected in the cluster classification based on the oceanographic data. Prior to ANOVA, homogeneity of variance was confirmed by Levene's tests. In addition, nonparametric Spearman rank correlation was used to explore the relationship between environmental variables and larval abundance of *U. pusilla* (early, middle and advanced stages of development). All Spearman rank correlations and ANOVA analyses were carried out with the SPSS statistical package.

Results

The hydrographical conditions have been reported in detail by Barton et al. (1998) and Navarro-Pérez and Barton (1998); therefore, only a brief description is presented. The cruise took place during the month with the strongest winds (August), and as a result of this forcing, many well-developed mesoscale features were evident in the area. During the study, a filament was present, originating on the continental shelf, near 27°N, and extending over 150 km north-westward towards the open sea (Fig. 1). The temperature distribution showed the complex oceanographic scenario of the Canaries CTZ, where upwelling filaments and eddies occurred at the same time. Specifically, at 25 m depth, the filament position is clearly delineated (Fig. 2a), whereas the temperature at 50 m evidenced the presence of a wide oval-shaped cyclonic eddy ($\sim$100 km) with its 17.5°C cold core around station 82 (Fig. 2b). This quasi-permanent eddy, trapped between the eastern Canary Islands and the African shelf, is responsible for entraining upwelled water around its periphery in a curved trajectory north-westward then southward, thus forming the filament (Barton et al. 1998). The ADCP currents showed a circulation pattern in which the filament flowed seaward at up to 0.25 m s^{-1} along the northern edge of the eddy, while to its south, the layers above 50 m were flowing shoreward with speeds over 0.35 m s^{-1} (Barton et al. 1998).

The classification of stations by dendrogram based on oceanographic variables revealed a high degree of spatial structure. Indeed, two main groups were categorized by an Euclidean distance of 12 (Fig. 3a). The first group included stations influenced by the African upwelling and the filament waters, whereas the other group comprised oceanic stations with well-stratified water column and stations located in the eddy (Fig. 3b). These two groups were used as factors to test the spatial differences in larval abundance.

In general, *Upogebia pusilla* larvae displayed a heterogeneous distribution in the study area, showing low abundance values and a close relationship with the upwelling front and the position of the filament (Fig. 4). The lack of significant differences between the abundance at night and day stations (ANOVA, $F = 2.29$, $P = 0.14$) indicates that the spatial distribution can be considered free from the interference of daily vertical migrations. Early larval stages (zoea I and II) of *U. pusilla* occurred mostly close to the shore, over the inner transect, with highest densities at stations 45 (12.3 larvae 100 m^{-3}) and 56 (20.1 larvae 100 m^{-3}). These larvae also appeared to undergo a slight advection north-westward, associated with the northern limb of the filament (Fig. 4a). Advanced larval stages (zoea III and IV) displayed a wider distribution reaching up to 150 km offshore. These intermediate larvae not only occurred over the shelf but also along the overall filament extension, with maximum values in the outer station 80 (14.6 larvae 100 m^{-3}) (Fig. 4b). The last stage of development (megalopa) showed lower densities than previous stages, with discontinuous cross-shelf distribution. The megalopae were present in the inner transect and in one

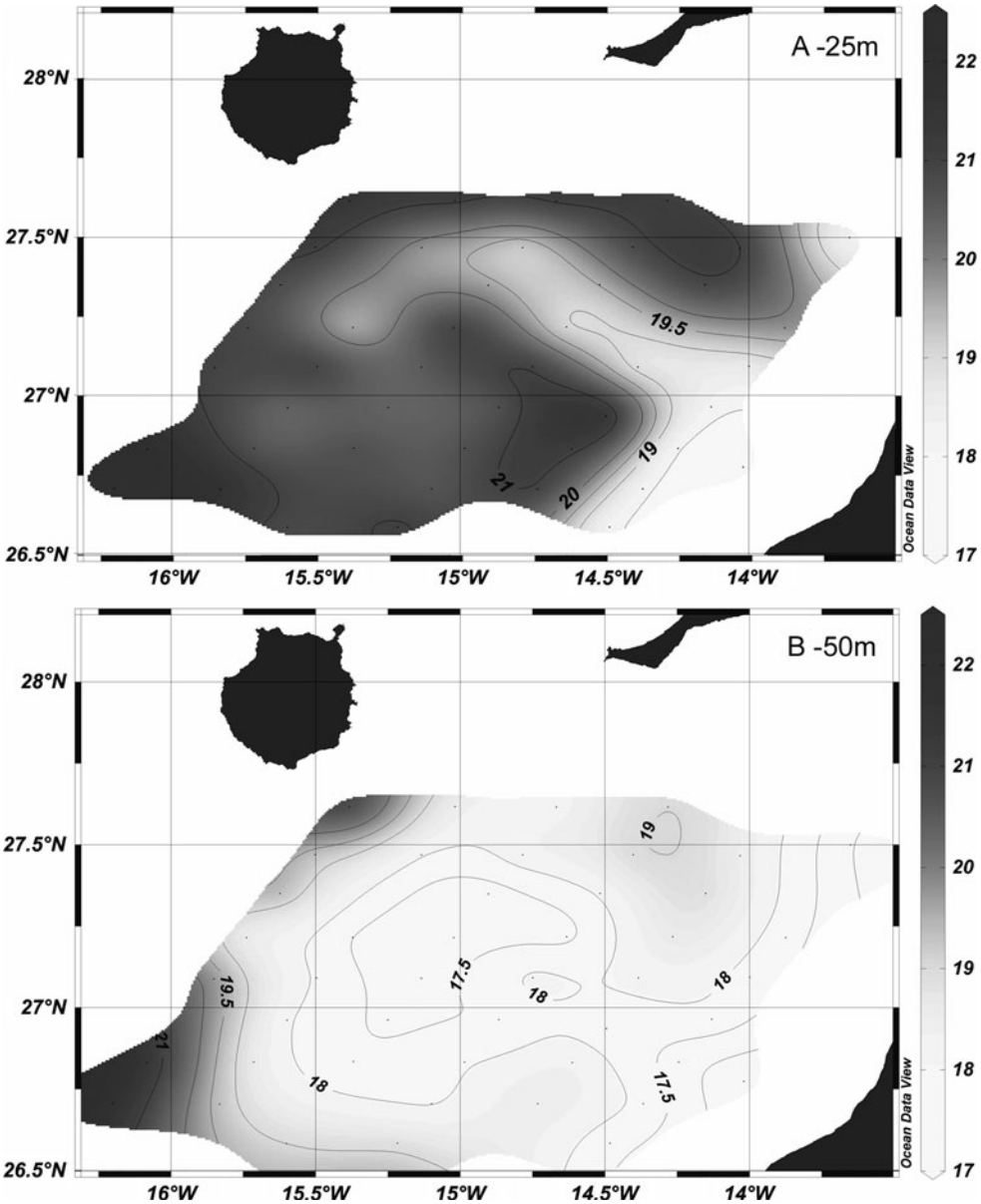

Fig. 2 Temperature (°C) distribution at 25 m (**a**) and 50 m depth (**b**). *Maps* have been generated using Ocean Data View, ODV (http://odv.awi.de/)

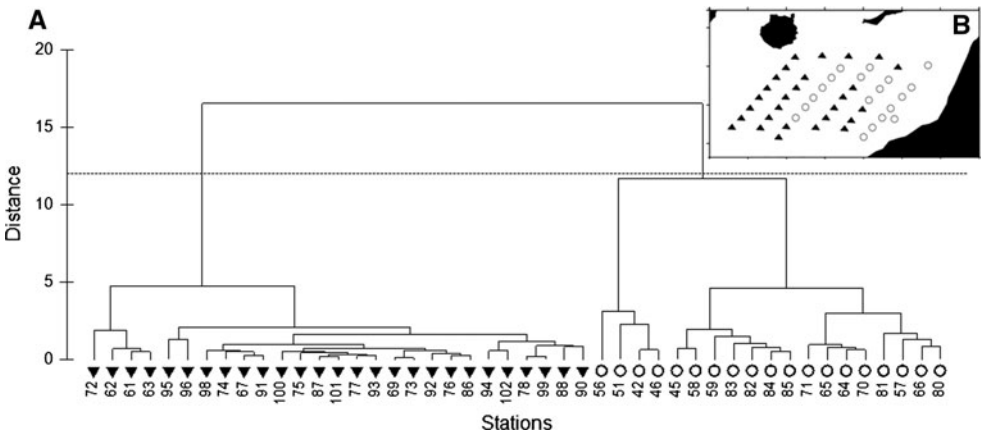

Fig. 3 **a** Hierarchical clustering dendrogram (using group-average linking) of 47 stations sampled based on oceanographic conditions. Two groups of stations were detected: those stations influenced by African upwelled waters (*open circles*), and the stations without influence of upwelled waters (*solid triangles*). (**b** *inset*) Geographical location of groups of stations as established by cluster analysis

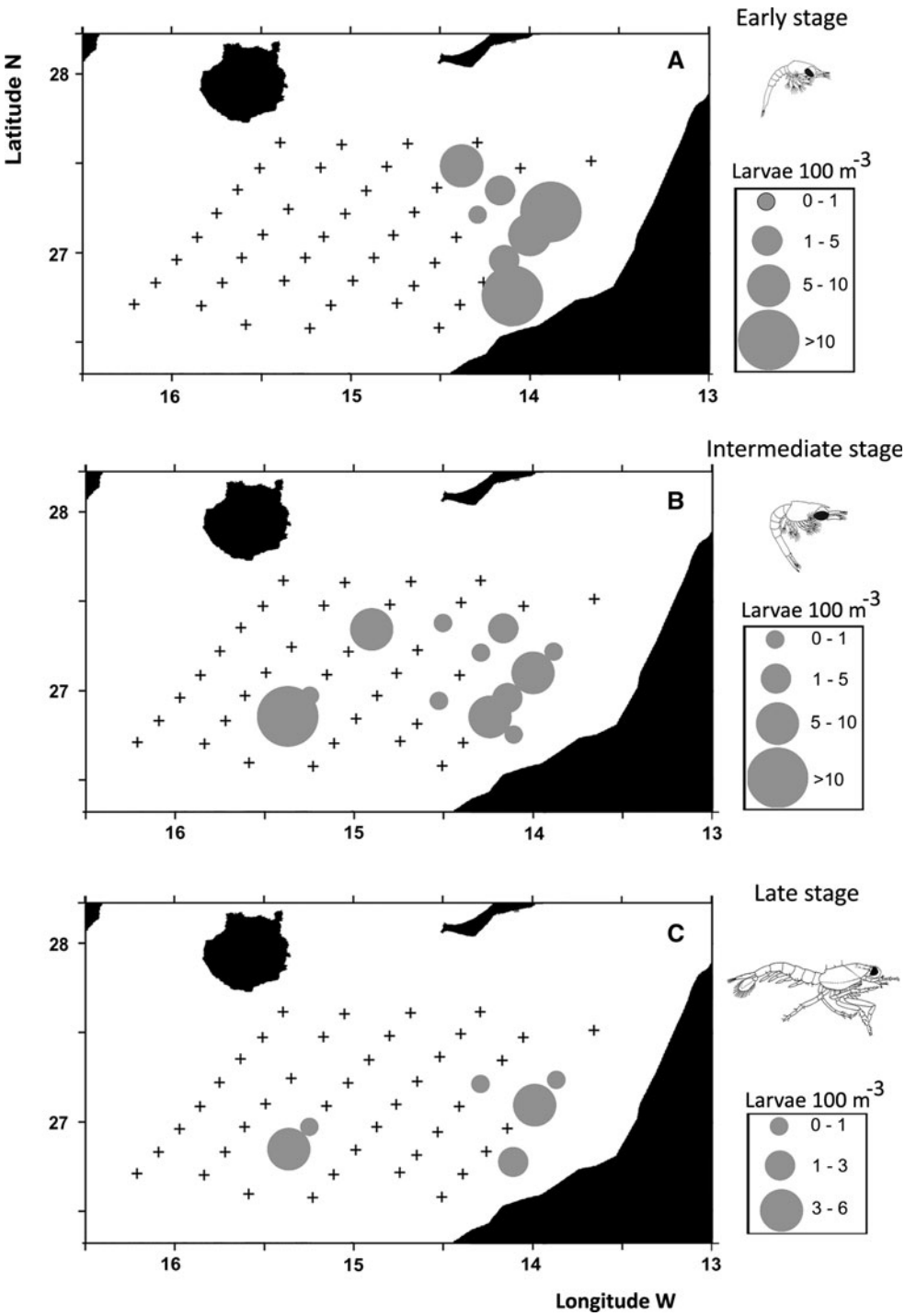

Fig. 4 Horizontal distribution of *Upogebia pusilla* abundance for **a** early stage, **c** intermediate stage and **e** late stage of development. Sampling positions are marked by +. Drawings are based on dos Santos and Paula (2003)

isolated maximum (4.1 larvae 100 m^{-3}) on the southern flank of the eddy, at station 80 again (Fig. 4c).

The strong correlation ($P < 0.01$) found between the abundance of early, intermediate and advanced larval stages corroborates the match with their spatial distribution (Table 1). All larval stages showed a distribution strongly associated with the upwelling front, which suggests that retention phenomena are occurring in this region. The results of the correlation analysis between oceanographic variables and larval abundances also supported the pattern observed in the distribution maps (Fig. 4). Temperature and salinity (SST, T25 m, T50 m, SSS, S25 m and S50 m) were negatively correlated with *U. pusilla* abundance, denoting a relationship between upwelled water (colder and less salty) and the presence of the larvae (Table 1). Indeed, early, intermediate and advanced stage larvae of

Table 1 Spearman correlation matrix between oceanographic variables and abundances of early, intermediate and advanced larvae of *U. pusilla*

	SST	SSS	T25 m	S25 m	T50 m	S50 m	Early larvae	Intermediate larvae
Early larvae	−0.44**	−0.39**	−0.39**	−0.44**	−0.19	−0.46**		
Intermediate larvae	−0.41**	−0.24	−0.31*	−0.34*	−0.36*	−0.51**	0.68**	
Advanced larvae	−0.40**	−0.14	−0.27	−0.23	−0.365*	−0.43**	0.57**	0.64**

SST sea surface temperature, *T25 m* temperature at 25 m depth, *T50 m* temperature at 50 m depth, *SSS* sea surface salinity, *S25 m* salinity at 25 m depth, *S50 m* salinity at 50 m depth. *$P < 0.05$; **$P < 0.01$

U. pusilla mainly occurred at nearshore stations with lower temperatures (17–20°C) and low salinities (36.32–36.45). Only few offshore stations with higher SST and SSS values showed positive abundances, related with the slight mixing at the boundary of the filament.

Finally, the analysis of variance (ANOVA) demonstrated that the abundances of *U. pusilla* larvae, in all stages of development, were significantly higher at the stations influenced by upwelling and filament structure than in the typical well-stratified oceanic waters (early stage: $F = 7.40$, $P = 0.009$; intermediate stage: $F = 8.03$, $P = 0.007$; advanced stage: $F = 5.58$, $P = 0.02$).

Discussion

It is often difficult to determine the source and fate of marine organisms, because their planktonic larvae spend considerable time developing in ocean currents that may transport them far from their natal populations (Morgan et al. 2009a). In our case, following the moulting cycle of *U. pusilla* larvae through the studied area, it is possible to discern information about their origin. The larvae displayed a horizontal distribution strongly influenced by the oceanographic processes. They were almost restricted to the African shelf and the oceanic area occupied by the filament structure. Therefore, the African coast seems the most probable origin of these *U. pusilla* larvae. Barton et al. (1998) observed that the position of this filament varied little in AVHRR and CZCS imagery during the weeks preceding the cruise. If we assume that the larval stages of *U. pusilla* last around 28 days (dos Santos and Paula 2003), the filament persistence during August 1993 can explain the presence of late larval stages (megalopa) at offshore stations. In addition, the advection pattern depicted by the mud shrimp larvae has almost exactly the same horizontal distribution as that observed for *Sardina pilchardus* larvae by Rodríguez et al. (1999) when they studied the ichthyoplankton on this same cruise. The larvae of *S. pilchardus* are considered a good tracer of the movement of African upwelled waters by filaments in this region (Bécognée et al. 2006; Moyano et al. 2009). Thus, the correlation between two larval patterns also supports the association with the filament.

U. pusilla inhabits the relatively shallow waters between the intertidal zone and 65 m depth (Udekem d'Acoz 1999), and consequently, one would expect the larval abundances of this mud shrimp to be concentrated nearshore and diminish seawards. This larval retention pattern of shallow-water crustaceans has been observed in the Portuguese (dos Santos et al. 2008), Californian (Morgan et al. 2009a, b, Shanks and Shearman 2009) and Chilean (Yannicelli et al. 2006a, b) upwelling regions. We observed higher larval concentrations in the upwelling front, but due to the nature of our study, we were unable to sample nearshore areas (<5 km offshore), which prevented the description of the complete larval distribution pattern of *U. pusilla*. We observed a long-distance transport (20–150 km), but the low densities suggest that only some larvae were affected by filament transport. The results from Shanks and Shearman (2009) and Morgan et al. (2009a, b) clearly demonstrated that larvae of intertidal invertebrates remain close to the coast during upwelling and downwelling periods. In particular, Shanks and Shearman (2009) found that high densities (10–100 larvae m^{-3}) of *Neotrypaea californianus* remained within 2 km of the coast and avoided seaward transport. Yannicelli et al. (2006b) reported even higher densities (up to 30,000 larvae m^{-3}) of *N. uncinata* in the entrance of a shallow bay. Considering this distribution pattern of *N. californianus* and *N. uncinata* (very common mud shrimps with similar habitat and distribution as *U. pusilla*), it is logical to think that the majority of the larval population of the *U. pusilla* was not sampled during the cruise because the peak of larval distribution most likely was in the nearshore waters of the African coast.

Determining the fate of these larvae that were dispersed offshore is also difficult. The filaments can sweep larvae far out to the open ocean without the possibility of finding suitable habitats in which to settle. As long as they remain in the oceanic area, they are exposed to strong predation pressure by diel vertical migrants in the ocean (Hopkins and Gartner 1992; Hernández-León 2008) that lead to a progressive decline and disappearance of the larvae. On the other hand, Barton et al. (1998) reported that a significant part of the offshore flow can return to the upwelling area by means of the cyclonic eddy around which the filament is entrained (Fig. 2). The cyclonic circuit, which has a

recirculation time of about 7 days, has been reported as a mechanism for the return of many fish larvae to the continental coast, their place of origin (Rodríguez et al. 1999), thus constituting an "ocean triad" (sensu Bakun 1998). The horizontal distribution of *U. pusilla* larvae suggests that larvae are also recirculated and retained in the filament–eddy system.

Other different transport scenarios reported for the Canaries CTZ concluded that the filaments can sweep larvae far to the open ocean without any possibility of their return to the African coast. Satellite images (Hernández-Guerra et al. 1993; Arístegui et al. 1997; Barton et al. 2004) have shown that eddies detached from the central and eastern islands of the Archipelago, occasionally interact with the offshore boundary of the filaments, entraining upwelled water and extending their transport much further westward. Several authors have observed that fish larvae displaced by the filament system can be transported towards the innermost islands (Rodríguez et al. 2004) to reach the coasts of Gran Canaria Island (Bécognée et al. 2006; Moyano et al. 2009). Therefore, if the larvae are able to avoid predation, the filaments could maintain a unidirectional gene flow between the invertebrate populations of the African coast and Canary Islands, playing a significant role in dispersal and connectivity.

Various authors have attributed the variations in recruitment of intertidal sea urchins, barnacles, mussels and crabs to oscillations in upwelling strength (Ebert and Russell 1988; Roughgarden et al. 1988; Connolly and Roughgarden 1998; Navarrete et al. 2005; Palma et al. 2006; Broitman et al. 2008). They observed lower recruitment rates near capes and headlands, preferred sites of upwelling filaments. The low larval densities of *U. pusilla* observed in the filament in our case suggests that only a small fraction of the larval pool is transported far from shore by this mesoscale structure. Therefore, recruitment variability of intertidal invertebrates might not be explained by local larval wastage due to advection in filaments. Sampling must be extended to the nearshore regions to contrast the fraction of intertidal larvae swept offshore by upwelling filaments with the fraction retained in the coastal area.

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