



Mechanisms for longitudinal transport on early life stages in benthic-pelagic fishes within a tide-dominated estuary

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ABSTRACT

Mechanisms that control the longitudinal transport of larvae and juveniles in nursery grounds such as estuaries are reported for some species. However, the behaviour and population consequences of these mechanisms are still uncertain. In this study, we tested selective tidal-stream transport from the along-channel (up- and down-stream) and cross-channel (from one margin to the other) perspectives for two kinds of fish: estuarine-resident gobies (*Pomatoschistus* spp.) and marine estuarine-opportunistic anchovies (*Engraulis encrasicolus*). Three cruises were conducted in the lower Guadalquivir estuary, on the ebb and on the flood of spring tides in summer. Plankton samples were collected across a channel section, at three stations (one in the middle of the channel and two in adjacent shallower areas), near the surface and near the bottom simultaneously. In addition, multiple physico-chemical variables (temperature, turbidity, dissolved oxygen, pH, salinity, chlorophyll-a, along with wind and current direction and velocity) were measured to examine the different correlations used by the studied fish in their strategies. The benthic distribution of gobies indicated that they used flood currents near the bottom of lateral (shallow) areas to ingress into and remain in the estuary, temperature and/or dissolved oxygen being their main possible cues. On the contrary, the anchovies were more abundant near the surface, especially on the ebb tide, showing downstream advection, which was mainly influenced by salinity. However, the largest individual anchovies in the lateral/shallow zones suggested a behavioural ontogeny, which, together with wind induced transport, could contribute to their retention. This comparison also enhanced the knowledge of the habitat distribution of two species common and abundant in estuaries, anchovies and gobies.

1. Introduction

A topic of special interest is how larval behaviours, especially depth and lateral preferences at an estuary section, along with periodic vertical or cross-sectional displacement, can promote the required longitudinal transport at each moment (advection up or down estuary) and retention in a selected zone or habitat within the estuary (Forward and Tankersley, 2001). Drifting meroplankton in water is a critical phase for the development of many species, as it determines their recruitment success (Cowen et al., 2006). During this period, transport processes depend on various biophysical interactions between regional hydrodynamic conditions, the spawning period, the supply of larvae and the natural

behaviour of each individual (Potter et al., 2015). The distribution of these organisms in the estuary is determined by multiple environmental conditions, the hydrodynamic regime being the main factor (González-Ortegón et al., 2012). Freshwater inputs, together with tidal flows, generate strong currents, which could be considered an extreme environment for fish larvae (Teodósio and Garel, 2015). Their ability to ingress up estuaries or to maintain their position in a given selected zone or habitat is challenged by the net (i.e., tidally averaged) flow, which is directed seaward (when averaged over a channel cross-section) and by the magnitude of the current, which frequently exceeds the larval swimming speed capacity (Teodósio et al., 2016).

According to De Wolf (1973), larvae could be retained in estuaries

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without swimming actively by mechanical transport in combination with tidal phases. In that sense, Creutzberg (1961) suggested the Selective Tidal Stream Transport (STST) hypothesis, in which larvae move up or down in the water column during the flood and ebb tides to accomplish their along-channel movement, taking advantage of the substantially greater velocities present at the surface than at depths, due to bed friction, can accomplish their longitudinal movements up or down estuary. Although the STST is widely accepted as the strategy by which larvae move into estuaries, other mechanisms have been proposed but are rarely evaluated in combination with other factors (i.e., Bardin and Pont, 2002; Hare et al., 2005). A combination of physical variables characterized by directional gradients, for example, water temperature, salinity, turbidity, and hydrostatic pressure, could act as synchronizing cues and induce tidal rhythms into larval movements (Boehlert and Mundy, 1988). Studies have discussed this behaviour for different species, such as fish (Burke et al., 1998; Hench et al., 2004) and invertebrate (De Vries et al., 1994; Hench et al., 2004) larvae, and even how ontogeny influences the perception of these cues (Teodósio et al., 2016). Most researchers have tested the STST in stratified estuaries, where the success of the mechanism is favored by pronounced vertical shear in velocities. In well-mixed estuaries, the velocity profile is more uniform along the water column (Fortier and Leggett, 1982), and fish larvae may need to adopt alternative (or complementary) strategies for successful ingress into estuarine nursery grounds. Other mechanisms proposed for upstream ingress include wind induced near surface transport, or residual inflows near the bottom or at the shallow margins (Roman and Boicourt, 1999; Simons et al., 2006; Morgan et al., 2011). Also, lateral movements have been considered as another strategy (Forward et al., 1999) because along-channel flow can feature pronounced lateral variability, depending on the bathymetry (Valle-Levinson and Lwiza, 1995).

The Guadalquivir is a well-mixed mesotidal estuary (Vanney, 1970) in the Gulf of Cadiz (Southwestern Iberian Peninsula). It has suffered extensive anthropic alterations from the 18th century onward, with the construction of numerous dams and river cuts (to facilitate vessel navigation) in the river basin, the substitution of marshes by agriculture fields, causing a reduction of the tidal flooding areas, etc. (Ruiz et al., 2015; Llope, 2017). The estuary is currently composed of a main channel with only a few tidal creeks, due to the significant reduction in intertidal areas. However, this estuary is considered the most productive in the region (Miró et al., 2020).

The early life stages of the fish community in the Guadalquivir estuary have been widely studied, the dry-warm season being the period with higher densities (Drake et al., 2007). The main species captured are the anchovy *Engraulis encrasicolus* (Linnaeus, 1758) and the gobies *Pomatoschistus minutus* (Pallas, 1770) and *Pomatoschistus microps* (Kroyer, 1838) (Baldó and Drake, 2002). The anchovy is a marine estuarine-opportunistic fish with offshore spawning in the Gulf of Cadiz (Baldó et al., 2006) and a larval maximum recruitment period from May to November in the Guadalquivir estuary (Drake et al., 2007). It is a commercial species important in the fishery sector of the region (Ruiz et al., 2017a). On the contrary, gobies are typical marine-estuarine species at temperate latitudes. Their seaward migration to reproduce during winter and early spring has been documented by several authors in different systems (Pampoulié et al., 1999; Guelinckx et al., 2008), although it has also been observed that this migration not ever happens (Bouchereau et al., 1991). In the Guadalquivir estuary such behaviour is unknown.

The objective of this study is to gain insight into additional mechanisms that can operate in combination with the STST to promote along-channel displacement of early life stages of fish. For this purpose, the movement strategies and the use of different zones in the channel were analysed for both the pelagic *Engraulis encrasicolus* and the benthic *Pomatoschistus* spp., together with potential environmental parameters that could trigger specific strategies. Specifically, the STST hypothesis was tested along with lateral migrations, water physico-chemical

characteristics, and wind effects using a Eulerian approach (e.g., over time in a fixed section of the estuary).

2. Material and methods

2.1. Study area

The Guadalquivir estuary is located at the southwest of the Iberian Peninsula, a warm temperate region with Mediterranean climate conditions. The estuary extends 110 km inland from its inlet in the Gulf of Cádiz (Atlantic Ocean; Fig. 1). It is a well-mixed mesotidal system that presents a convergent structure with widths of 800 m near the mouth and 150 m at the head (Díez-Minguito et al., 2012). The morphology of the estuary consists of a single channel with a main navigable channel of 7.1 m average depth (Ruiz et al., 2015). The river discharge is generally low as it is controlled by the Alcalá del Río Dam; for example, the mean discharge was 22.3 m³/s in 2017 (SAIH Confederación Hidrográfica del Guadalquivir, <http://www.chguadalquivir.es/saih/DatosHistoricos.aspx>).

2.2. Biological sampling

Sampling was carried out during the summer of 2017, during three different cruises on spring tides. Each sampling cruise was performed near the peak ebb and flood currents (see Figure S1) on two consecutive days in daylight (June 12–13, July 11–12, and August 9–10, 2017). The samples were collected with a passive haul from an anchored boat. Three different stations were surveyed across a channel section, 13 km upstream from the mouth: two shallow stations were located near the (west and east) margins (water depths 4.2 m at high tide and 2.2 m at low tide), and a third station was in the middle of the channel at a depth of 6.8–8.8 m at low and high tide, respectively (Fig. 1). The near surface and bottom layers were sampled simultaneously to determine vertical variations in the early fish distribution. A plankton net of 60 cm diameter and an epibenthic sledge trawl of 43 × 60 cm, both with a mesh size of 500 µm, were used for subsurface and bottom sampling, respectively. Each net was equipped with a flow meter (2030R General Oceanics), and the volume filtered per tow was 90 ± 27 m³. The trawl had a stragulation mechanism, which was released once it reached the bottom to keep the net closed during the up and down movement of the tow. At these two layers (surface and bottom), four samples were collected at each cross-channel station in every tidal phase (ebb and flood); this sampling strategy was replicated for each cruise. In total, 144 tows were conducted, 48 in every cruise. The samples were fixed in 70% ethanol, and the early stages of *E. encrasicolus* and *Pomatoschistus* spp. were sorted. Furthermore, in the case of *E. encrasicolus*, due to the presence of individuals in different stages of life (postlarvae and juveniles), their total length was measured using an image-analysis system, where the individuals were scanned and measured with the software ImageJ. Such analysis was not performed on *Pomatoschistus* spp. since the samples featured no differences in sizes (total length of 30 mm approximately) and life stages (all individuals were in juvenile development).

2.3. Physico-chemical data collection

Simultaneously with every biological sampling, water properties and current velocity were recorded along the water column. The depth, temperature, salinity, turbidity, dissolved oxygen (DO), chlorophyll-a (Chla) and pH were collected at 1 Hz with a multiparametric probe (Eureka Manta2). Current velocity was measured with an Acoustic Doppler Current Profiler (ADCP 1 MHz – Aquadopp Profiler Nortek) installed on the boat (i.e., looking down). The ADCP was used in bottom-tracking mode, and velocity profiles were obtained as ensembles averaged over 120 s in cells of 0.5 m thick.

Wind speed and direction data were provided at 5-min intervals by the meteorological station Vetalengua, located 7 km northwest from the

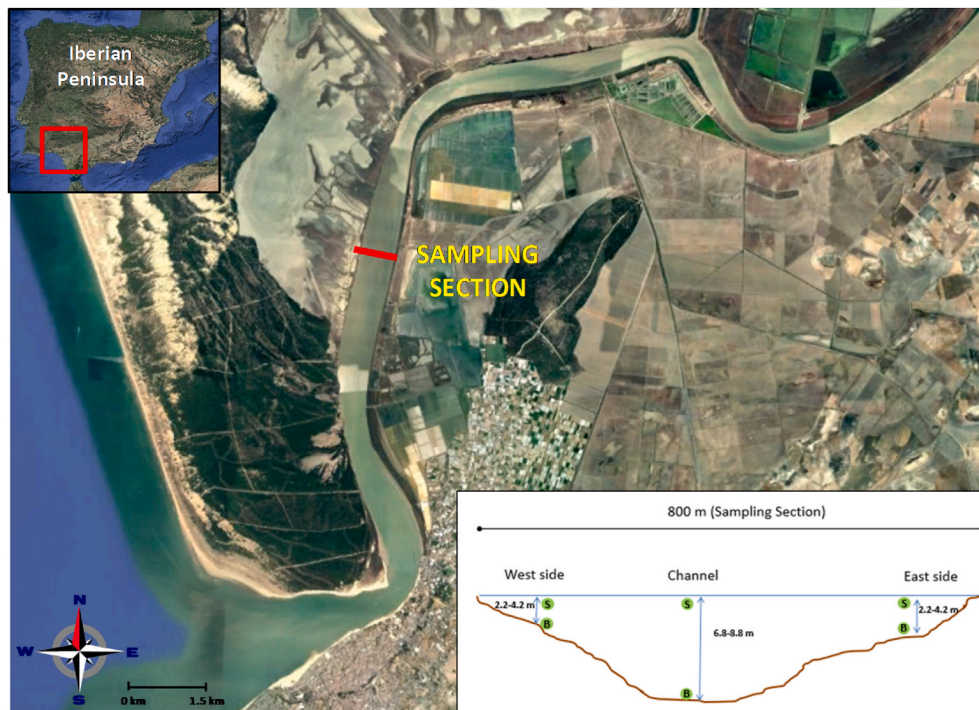


Fig. 1. Sampling station locality and cross-sectional scheme with the stations and depths (S: surface; B: bottom). Bottom depth and distance across are not to scale but are plotted in an approximate proportion of 1:20.

sampled section ($6^{\circ}22' 55.96381''\text{W} - 36^{\circ}55'21.93697''\text{N}$), from the Spanish National Research Council (CSIC-EBD-ICTS).

2.4. Data analysis

The measured variables (including the current velocity) during each sample tow were averaged into a single value over the first meter for surface samples and the last meter for bottom samples. The results of all environmental variables were represented as boxplots, with discrimination of the water depth, tidal phase (i.e., ebb or flood), and station (i.e., west, channel, east) using the package “ggplot2” of R 3.5.2 software (R Core Team, 2018).

Physico-chemical variables were organized into a variable/sample matrix and a Euclidian distance similarity matrix was calculated with normalized data. Differences in the multivariate structure of environmental variables were analysed using distance-based permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001; McArdle and Anderson, 2001). When the number of total possible permutations to obtain the p-values was low, we used the estimate obtained by Monte Carlo sampling (Anderson and Robinson, 2003). The experimental design included three crossed fixed factors: depth (two levels, “Surface and Bottom”), tide (two levels, “Flood and Ebb”), and station (three levels, “West side, Channel and East side”); and two random factors: cruise (three levels, “June, July, and August”), orthogonal to the three previous factors, and sampling time (four levels, “1–4”) nested within tide, station, and cruise. This last factor is a random block used to consider simultaneous samples taken in the surface and bottom layers; in this sense, this is a “randomized block design,” and it was analysed following the general consensus of excluding the interaction term between “depth” and “sampling time” from the analysis (Anderson et al., 2008). When appropriate, significant terms with more than two levels were analysed using a pairwise comparison with the PERMANOVA test. Additionally, patterns in environmental variables were represented graphically using a plot of the two first principal axes of a Principal Component Analysis (PCA). Multivariate analyses were performed using the software PRIMER v6.1.11 and the PERMANOVA + v1.0.1 statistical

package (Clarke and Gorley, 2006).

To assess the influence of advection on fish transport, speed and direction of water current and wind were analysed separately. The velocity vectors were rotated in the along- (positive upstream) and across-estuary (positive eastward) components according to the estuary main orientation (i.e., 10°E from north). Wind speed and direction for each sampling day were averaged during the sampling time of each tidal phase (i.e., the ebb and flood tides). Currents were represented as scatter plots with the package ‘ggplot2’, while wind condition were displayed as rose plots with the package ‘openair’ in R software (R Core Team, 2018).

To investigate the factors driving the strategy used by the studied species to move across the estuary section, two generalized linear mixed-effects models (GLMM) were run with counts of *E. encrasicolus* and *Pomatoschistus* spp. as response variables. The most suitable distribution for these data was the negative binomial, and the model was fitted with the function ‘glmer.nb’ of the package ‘Lme4’ (Bates et al., 2015). The design of the categorical factors used was the same as that used for the multivariate environmental analysis (fixed factors: depth, tide and station; random factors: cruise and sampling time). Water properties (temperature, salinity, turbidity, DO, Chla, pH) and current velocity were also used as explanatory variables, in addition to the filtered volume as an offset variable.

The first step of the model selection process to determine the best fitting GLMM was to create a global model with all predictor variables included (Bates et al., 2015). Previously, one of the variables that showed a similar or complementary pattern in PCA was excluded (dissolved oxygen [negatively correlated with temperature] or chlorophyll-a [positively correlated with turbidity]) from the analysis to avoid collinearity. The multicollinearity of the selected variables was further analysed using variance inflation factors (VIF) with the function ‘vif’ from the package ‘car’ (Fox and Weisberg, 2011); all variables in the global model had a VIF <3 . We performed information-theoretic model selection based on Akaike’s information criterion (AIC; Akaike, 1974) and Akaike weights (Burnham and Anderson, 2002) using the function ‘dredge’ of the ‘MuMIn’ package (Barton, 2018). The model with the highest-adjusted Akaike weight was considered the best-fit model used

for the analysis (Burnham and Anderson, 2002). Finally, significant categorical terms in the best-fit model with more than two levels, were analysed using pairwise comparison with the package ‘emmeans’ (Lenth, 2018).

The total lengths of the anchovies were compared between different depths of water, tidal phases, and stations of each cruise to test whether individuals of different sizes used distinct strategies. For this analysis, linear mixed-effects models (LMM) were run using the function ‘lmer’ of the package ‘lme4’ with a Gaussian distribution. In this case, the global model had three crossed fixed factors (depth, tide, and station) and one random factor (cruise). The model selection process and post hoc analysis of the best-fit model were similar to those explained above.

3. Results

3.1. Environmental analysis

PERMANOVA showed different physicochemical conditions of the samples in the estuary section between depths and tides, as well as stations and tides throughout the cruises (Table 1). Pair-wise analysis of significant interactions showed differences between the surface and the bottom in both tidal conditions, and also between the stations during the flood, the east and west sides margins distinct from the channel, although only the west side was significantly different (Table 2).

The PCA analysis showed a clear pattern associated to tide cycles: the current velocity and DO concentration were higher on the ebb tides, and the temperature and pH were higher on the flood tides (Fig. 2). Also, high levels of turbidity and chlorophyll-a were observed at both margins. On the other hand, depth comparisons showed a slight vertical stratification of some environmental variables (Figure S2) with higher relative values of temperature and current velocity in the surface layers, while the turbidity, salinity, and chlorophyll-a were larger at the bottom depth.

In addition, wind data (Fig. 3) showed a dominant direction from west-southwest to east-northeast in most flood tides, except for the last sampling day. However, no clear patterns were found during the ebb tides, where some sampling days had a direction from east-northeast to west-southwest and other days from south-southwest to north-northeast.

The currents showed a similar directional pattern (Fig. 4) during the flood tides with a dominance of the east direction for all cruises, particular in August which is the sampled period with strongest winds. Contrary, a trend to west current direction was observed during the ebb tide (mainly June and July cruises) except for August. In all cruises, the

Table 1

PERMANOVA results of environmental variables. Df: degree of freedom; SS: sum of squares; MS: mean sum of squares.

Source	df	SS	MS	Pseudo-F	P (perm)
Depth	1	60.041	60.041	21.206	0.0876
Tide	1	108.87	108.87	5.4735	0.0189
Station	2	22.847	11.424	1.2642	0.3214
Cruise	2	209.98	104.99	19.559	0.0001
DepthxTide	1	22.221	22.221	11.275	0.0301
DepthxStation	2	1.8788	0.93939	0.73702	0.5997
DepthxCruise	2	5.6739	2.837	2.5216	0.0208
TidexStation	2	44.411	22.206	4.7071	0.0086
TidexCruise	2	39.877	19.938	3.7144	0.0027
StationxCruise	4	36.2	9.05	1.686	0.0729
DepthxTidexStation	2	7.7155	3.8578	2.5679	0.1281
DepthxTidexCruise	2	3.9475	1.9738	1.7544	0.1018
DepthxStationxCruise	4	5.1005	1.2751	1.1334	0.3214
TidexStationxCruise	4	18.861	4.7151	0.8784	0.5533
Station	48	257.66	5.3678	4.7711	0.0001
(StationxTidexCruise)					
DepthxTidexStationxCruise	4	6.0147	1.5037	1.3365	0.2
Res	48	54.003	1.1251		
Total	131	917			

Table 2

Pairwise analysis of significant interactions. *p estimation obtained by Monte Carlo sampling.

Term 'TidexDepth'	Ebb		Flood	
Groups	t	P(perm)	t	P(perm)
Surface-Bottom	7.0251	0.0002	3.3084	0.0023
Term 'TidexStation'	Ebb		Flood	
Groups	t	P(perm)	t	P(perm)
East, West side	1.5361	0.1245	1.1316	0.3481
East side, Channel	1.308	0.2555	2.151	0.0533
West side, Channel	0.87768	0.5824	2.182	0.0441*

stations showed similar directional patterns and the speed in the surface layers was faster than in the bottom.

3.2. Biological analysis

Engraulis encrasicolus and *Pomatoschistus* spp. were the most abundant and consistently present with a total of 11.676 (79%) and 2.695 (18%) individuals sampled, respectively.

3.3. *Pomatoschistus* spp.

Fig. 5A shows the densities (ind./1000 m³; mean ± SE) of *Pomatoschistus* spp. by function of the tide, depth, and station averaged across all cruises. The best-fit model (Table S1) showed significant differences with depth: gobies were present mainly at the bottom and were very scarce at the surface. In fact, on the surface, due to the low general density, there was no clear pattern and no significant differences between the tides or stations. Instead, in the bottom, density differences were found between the ebb and flood tide on both margins. Also, a different global pattern was found between the flood and the ebb: during floods, densities were significantly higher at the two margins compared to the channel; during ebbs, there was a density gradient, increasing from west to east, and the density on the west side was significantly lower than at the remaining stations. The GLMM analysis also showed a slightly positive relationship between temperature and goby density (Table S1). This relationship can be graphically observed in Figure S3A, as well as some associations with higher turbidity, chlorophyll and pH, as expected during flood.

3.4. *Engraulis encrasicolus*

Fig. 5B shows the densities (ind./1000 m³; mean ± SE) of the anchovy *E. encrasicolus* according to the depth, tide, and station averaged for all cruises. The best-fit model (Table S2) showed significant differences with depth: anchovies were mainly at the surface and were very scarce at the bottom, opposite to the spatial distribution of gobies. In fact, similar to what we found in gobies but at the opposite depth (in the bottom), there were no significant differences between stations, although small but significant differences were found between tides. Instead, at the surface, significant differences were found between tides and stations: there were higher densities during the ebb compared with the flood, and there were higher densities on the east side than at the other stations.

The GLMM analysis also showed that salinity was the only environmental variable with a significant influence on anchovy distribution along samples (Table S2). A negative relationship was found, the low salinity range (19–27 PSU) being associated to a higher number of anchovies, mostly in the surface samples. This is also in agreement with the trend to find higher densities with higher oxygen concentration observed in Figure S3B.

The total length of anchovies ranged between 15 and 40 mm, and most of the individuals were in post-flexion state with developed fins.

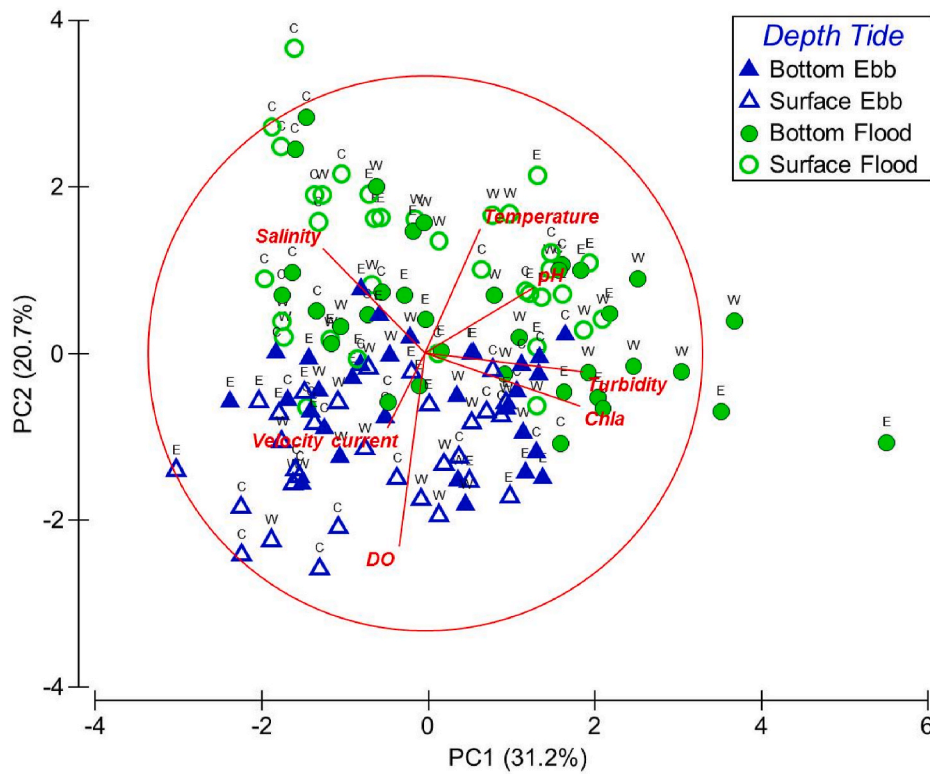


Fig. 2. Plot of the two first principal components of a PCA with environmental variables (DO: dissolved oxygen; Chla: chlorophyll-a; W: west side; C: channel; E: east side).

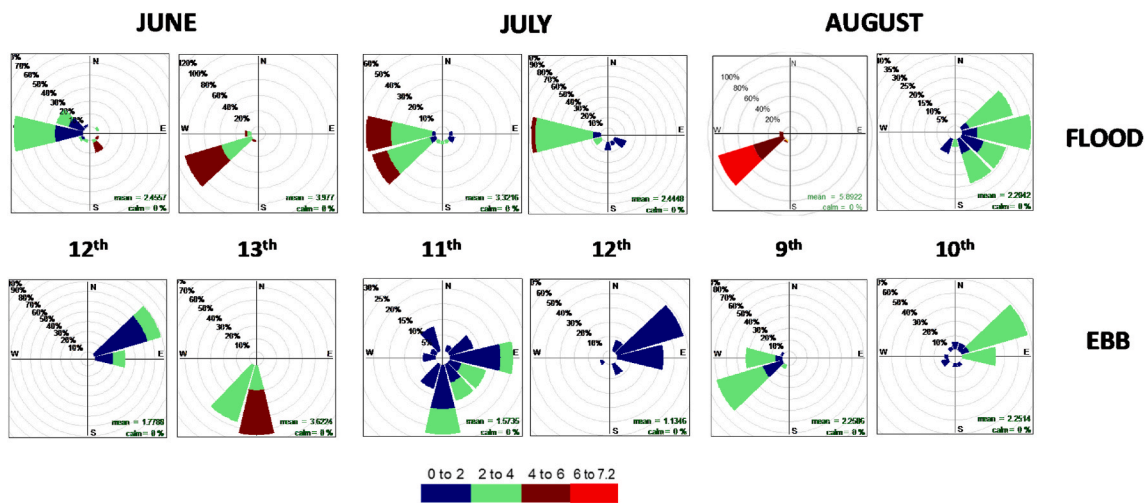


Fig. 3. Wind rose plots with speed and direction data of Vetelengua Station during every sampling day in each tide condition.

The best fit LMM (Table S3) showed that the mean total length of the anchovies varied with depth, tide, and station (Fig. 6). Flood conditions were associated with larger sizes than the ebb tide; during the flood, larger sizes were found at both margins (east and west) compared to the middle of the channel; during the ebb tide at the surface, mean size on the east side and channel was slightly but significantly higher than on the west side.

4. Discussion

Different mechanisms were observed for anchovies and gobies in their movement along the estuary, and the differences found in physico-chemical variables across the estuary section and along the tidal cycle

could serve as cues to lead their strategies.

4.1. Environmental conditions

Although, from a hydrological point of view, the Guadalquivir is defined as a well-mixed estuary (Vannay, 1970), from a biological point of view, the surface-bottom differences in physico-chemical variables across the channel could be detected by fish larvae, guiding them through different pathways within the estuary. The estuary section sampled is tide-dominated (Díez-Minguito et al., 2012), which could provoke periodic and slight stratifications (Díez-Minguito et al., 2013) during the tidal cycle. Tidal asymmetry has previously been shown in the middle of the channel, where the estuary is flood-dominated

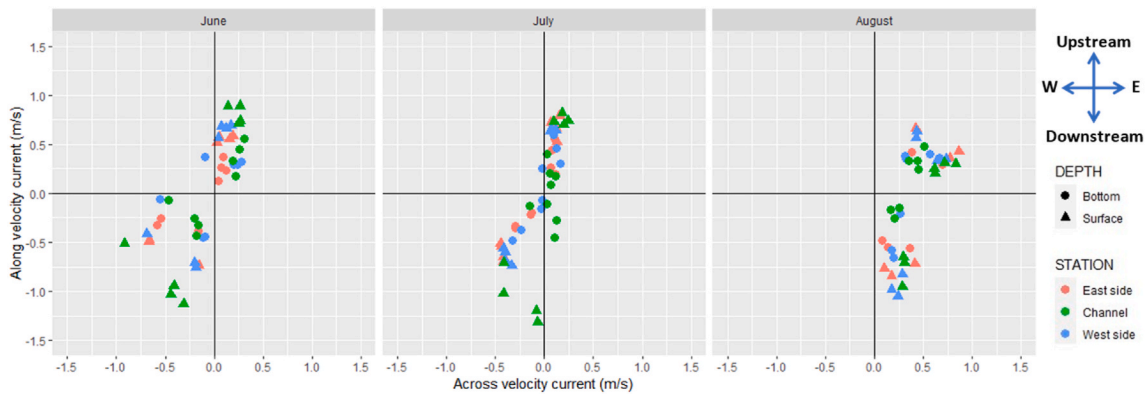


Fig. 4. Water current velocity along (positive upstream) and across (positive eastward) the channel of the Guadalquivir estuary. The colors indicate the sampling stations (red: east; green: channel; blue: west) and the markers indicate the sampling depth (bottom: circle; surface: triangle). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

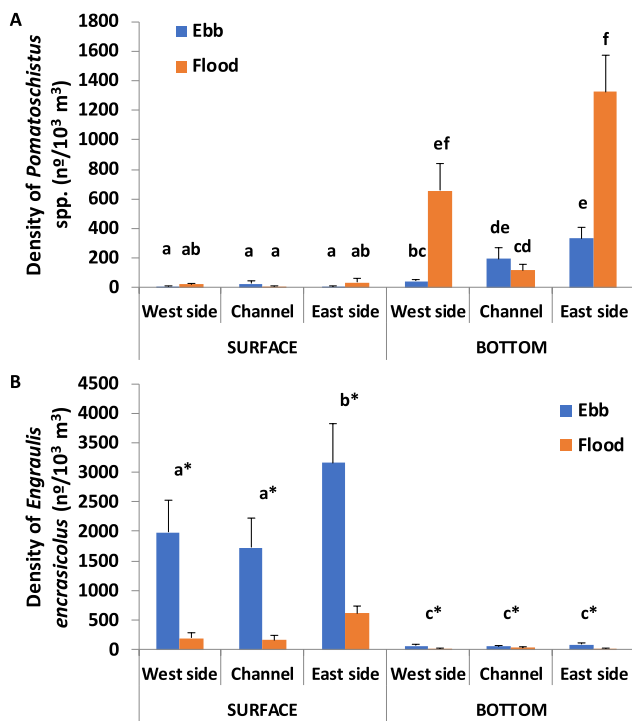


Fig. 5. Density (mean \pm SE) of *Pomatoschistus* spp. (A) and *Engraulis encrasicolus* (B) in different stations along all cruises. A) Different letters indicate post-hoc significant differences ($p < 0.05$) among cells of the three-way interaction “Depth x Tide x Station”. B) Different letters indicate post-hoc significant differences ($p < 0.05$) among cells of two-way interaction “Depth x Station”; Asterisks (*) indicate significant differences ($p < 0.05$) among tides within the same station.

(Díez-Minguito et al., 2012). However, in our study, higher maximum current velocities were measured during the ebb tide on the surface than in flood tide samples, mainly at the channel station, probably due to the proximity of the section to the estuary inlet (Garel, 2017). Nonetheless, the dominance of the tidal flow near the margins (out of the navigation channel) of the Guadalquivir estuary is unknown. Yet, the significant eastward cross-channel component during all the floods sampled in this study indicates potential lateral differences in the net flux (up- or downstream) of water as reported in similar estuaries (e.g., Garel and Ferreira, 2013). In addition, current direction seems to be influenced by the wind as both variables showed the same pattern, at least during the

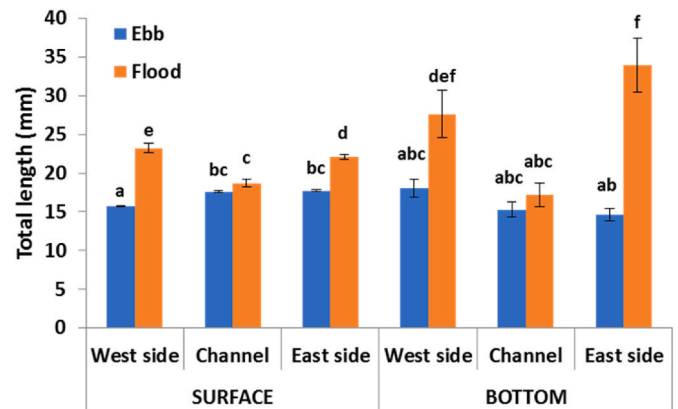


Fig. 6. Total length (mean \pm SE) of early life stages of *Engraulis encrasicolus* in different stations along all cruises. Different letters indicate post-hoc significant differences ($p < 0.05$) among cells of the three-way interaction “Depth x Tide x Station”.

flood, and even in some cases during the ebb. In fact, during summer, southwesterly sea breeze typically blows during the afternoon in the region (Folkard et al., 1997), which could promote upstream flows, in particular at the more exposed eastern margin.

DO and temperature were, as expected, negatively correlated and played a major role in the differences found, especially between tides. Lateral variations in the bathymetry could affect the water circulation (Valle-Levinson and Lwiza, 1995). According to Li and O’Donnell (1997, 2005), the distinct water depth over the shoals and the channel results in more asymmetrical tides over the shoals, where the bed friction experienced by the flow is stronger, which in turn produces a residual flow landward in tidally-dominated estuaries with weak of river discharge like the Guadalquivir (Cáceres et al., 2003). This inflow is compensated by a seaward flow over the channel, where the bed friction is weaker. Another effect of the different current velocities was the observed larger salinity range in the channel than at the margins as a result of advection producing cross-channel salinity gradients (Nunes and Simpson, 1985). Besides, the shallow water depth near the margins typically enhances both sediment and microphytobenthos resuspension, in agreement with the higher turbidity and chlorophyll-a concentration observed in these areas (Díez-Minguito and de Swart, 2020; Miró et al., 2020).

4.2. *Pomatoschistus* spp.

Gobies of the *Pomatoschistus* spp. are benthic species that show a clear bottom-dwelling behaviour, remaining deep in the water column

at all times of the tide cycle as do other species, for instance, *Microgobias undulates* (Boehlert and Mundy, 1988). The use of vertical migrations between the surface and bottom layers to relocate along the estuary, as proposed by the STST hypothesis, seems not to be applicable here. They must therefore be using an alternative strategy. The near bed current velocities were weak enough to allow movement against the current or lateral migration. Experimental studies of critical swimming speed in other species of gobies with a similar total length showed values around 0.4 m/s (Donaldson et al., 2013), which are higher than most of the water current velocities recorded with the ADCP in the bottom during the different tidal phases and cruises. However, the critical swimming speed cannot be maintained for long periods through the tidal phase, in particular around peak flows. The higher densities found on the flood tides may indicate an ingress strategy. Related to its benthic lifestyle in adult stage, their locomotion is described as short hops and darts, remaining close to the bottom and frequently resting on it between darts, being propelled by combined adduction of the pectoral fins and tail beating (Asriaens et al., 1993). In addition, Magnhagen and Forsgren (1991) described burrowing behaviour of these species as a method to avoid different kinds of risky situations, which could also be used to avoid undesirable water currents. Combining these behaviours with their swimming capabilities could force these species to select more suitable environments (i.e., flood tide and bottom depth) for ingress and maintenance into the estuary; however, this requires confirmation.

Furthermore, some authors (e.g., Pampoulie et al., 1999; Guelinckx et al., 2008) have described seaward migrations taking place in other regions during the early spring for the purpose of reproduction. In that case, in the summer season, when the study was carried out, individuals could be entering up the estuary through the bottom layers to reach the upper zones using flood-tide transport (Forward and Tankersley, 2001), which could partially explain the density differences found between tidal phases. Additionally, their higher presence in the shoals would make their upstream ingress more efficient than ingress by the channel (Scully and Friedrichs, 2007), where the longer ebbs delay the beginning of the flood tide and increase the flushing-out time (Díez-Minguito et al., 2012).

Different studies have observed the influence of temperature on the recruitment phenology and coastal migration of *Pomatoschistus* spp. (Pampoulie et al., 1999; Dolbeth et al., 2007). Our study, despite the limited temperature range, showed a significant and positive relationship between this variable and the abundance of gobies. Besides, due to the negative relation between temperature and DO, without an experimental study under controlled environmental conditions, it is not possible to determine which of these two variables is the potential behavioural cue in gobies. Also, DO has been shown to affect the behaviour of *P. minutus*, increasing their swimming activity to avoid concentrations lower than 3.5 mg O₂/L (Petersen and Petersen, 1990). However, we did not register concentrations lower than 5 mg O₂/L; therefore, it is likely that temperature could act as the main cue in this case. Notwithstanding, during this study, higher mean temperatures and lower DO values were recorded during the flood together with higher densities of gobies. Both variables, separate or combined, could act as cues for these species to go along with the flow up or downstream. Hence, when gobies detect water masses with higher temperatures, they could follow the current to ingress or reach upstream zones of estuaries, and contrary (lower temperature) to egress (reverse strategy with the dissolved oxygen).

4.3. *Engraulis encrasicolus*

The anchovy *E. encrasicolus* is a pelagic species that remains in the surface layers throughout the entire tide cycle. As with gobies, the STST hypothesis would not be applicable in this case, as previously reported for another anchovy species (Schultz et al., 2000, 2003). There is likely an alternative strategy in use. The consistently higher densities on the ebb than on the flood, were previously observed in the Guadalquivir

estuary during daylight and night (Drake et al., 2007). This pattern was interpreted as an indication of tide-related lateral migration to shallower, more productive areas during high tide for feeding, as previously observed in other nursery areas in the region (Drake and Arias, 1991). The present study was specifically designed to detect vertical or lateral migrations, complementing this previous knowledge. Clear evidence of lateral migration would imply a significant interaction between “tide” and “station” (a different relative density in lateral stations with respect to the channel between ebb and flood) but not a global reduction in density during flood both in the lateral stations and in the central channel, as observed.

The higher densities of anchovy during ebbs on every cruise suggest that larvae and juveniles not collected during the flood tides must be using a different zone in the river section to move upstream [a certain dilution effect, because of the higher volume in high tide, can explain a small part of these differences (Strydom and Wooldridge, 2005), but it would not explain the notable differences found]. The possibility of lateral migration still exists, as anchovies could be using the shallowest zones, not accessible by boat, during high tide (a different approach would be necessary to explore this possibility, such as the use of fixed traps). In fact, when the water spreads over the shoals during a flood tide, larvae and juveniles would be transported over these zones as Jager (1999) suggested for flounder. An indication for this process was described in another nursery area in this region (i.e., Cádiz Bay), where juveniles and larvae ingress small intertidal channels with every flood tide (Arias and Drake, 1990). In the Guadalquivir estuary, provided that the intertidal marshes were mostly transformed and isolated from the main river, small fish would accumulate in the shallowest zones. The higher densities found in the margins (mainly on the east side) suggests that, other than passive transport by water spreading over the intertidal flats, larvae would tend to remain in these areas. Indeed, the larger sizes found in the margins indicate that individuals with a higher swimming capacity, that can better swim against the ebb tide returning into the channel, would also be able to remain more effectively near the margins.

In this regard, the highest densities found were always on the east side, coinciding with the wind direction during most cruises in flood tide conditions (southwesterlies), which could drag the surface water layers, and consequently the suspended organisms, toward this margin. Schieler et al. (2014) showed that the wind can induce the transport of larvae, in their case from the nearshore into the estuary. Indeed, current showed a significant eastward cross-channel component in most of the cruises supporting this hypothesis. Therefore, a possible mechanism for directional transport would be: the persistent and frequent westerlies during the flood, which push the surface water layers to the east margin, transport most anchovies toward that side, gathering in the shallowest areas (not possible to sample with the anchored boat) where they are displaced upstream; when the tide changes to the ebb condition, the currents with the western direction transport individuals downstream as well as distribute them throughout the entire channel section (always on surface water layers), leaving more abundance in the east side for proximity where they accumulated. In addition, the most developed individuals would also accumulate in the margins, where the current speed is lower, and they could better manage their strategies. This hypothesis needs to be corroborated.

Alternatively, Schultz et al. (2003) suggested a slight net ingress upstream using vertical migrations to mid-depth of the water column. Whether anchovies made different use of mid-depth in the main channel (in lateral samplings, the distance between the surface net and the epibenthic sledge was negligible) remains to be verified. However, we did not find a significant decrease in current velocity or any other environmental variable that could justify a very different pattern in this station. Furthermore, anchovies have a positive phototropism, and light attenuation is strong in the Guadalquivir estuary due to high turbidity (Ruiz et al., 2017b) which would tend to lead them to the surface.

In general, considering both this study and the information already available for this estuary, no clear mechanism for anchovies to progress

upstream into the estuary has been evidenced. Lateral shallowest areas, where higher densities and larger sizes have been found, typically feature weak flows (see, e.g., Garel and Ferreira, 2013). This would allow anchovies to swim more efficiently against the current and to better control their position in particular on neap tides. The present study and Drake et al. (2007) were carried out on spring tides, when tidal flows are almost twice those on neap tides (Díez-Minguito et al., 2012). Several studies have found different abundances in the exchange between spring and neap tides (Pollock et al., 1983; Tanaka et al., 1989; Strydom and Wooldridge, 2005), and the importance of neaps for the ingress of some species into the estuary should be verified: anchovies could have a net downstream transport on spring that could be compensated during neaps, using shallower areas as proposed by Teodósio and Garel (2015). This kind of current circulation and the lower velocities could facilitate the intrusion of anchovies, which are attracted upstream by lower salinity levels (as observed in this study) or even swim against weak currents as described by Patrick and Strydom (2014) for other fish larvae and juveniles. In fact, physico-chemical changes between stations during flood tides, such as the shift in water current velocity and its consequent salinity variations, could function as signals in this species. Thus, an ontogenetic transition in behavioural capability (Teodósio and Garel, 2015) comparable to sense acuity and behavioural hypothesis of Teodósio et al. (2016) could be occurring inside of the estuary.

4.4. General patterns

Anchovies and gobies are common species that usually dominate the early life stages of fish assemblages in temperate estuaries all around the world (Bouchereau and Guelorget, 1998; James et al., 2007). Their distribution in estuaries has been widely studied, anchovies being pelagic species and most of the gobies, benthic ones. The results obtained show that these species may have opposite strategies to move along a section of the estuary. In addition, different physico-chemical variables were found to influence their distributions across the estuary section. For a marine estuarine-opportunistic species, such as *E. encrasicolus*, salinity generally presents an essential signal to detect estuaries (Elliott et al., 2007). Estuarine resident species, such as the *Pomatoschistus* spp., are euryhaline organisms with a wide range of salinity tolerance (Souza et al., 2014), and values within the range recorded in this study (19–32 PSU) seem not to be particularly important for their distribution throughout the estuary section. In contrast, variables such as temperature and/or DO, which also exhibit a wide range of variation in estuaries, seem to be more relevant.

Notwithstanding, both species presented the same transversal zonal pattern with higher abundances on the east side, which coincided with the current and wind directions during most cruises in flood tides (southwestern to northeastern). The upstream advection promoted by these conditions (in particular east margin) might facilitate the ingress and upstream transport of both species and even other small organisms. Wind, in addition to other factors such as bathymetry, tide, water flow, or density-driven, could influence the residual axial landward current (or provoke a lower net seaward velocity) (Hare et al., 2005; Yamaguchi and Kume, 2008). In fact, Díez-Minguito et al. (2014) showed that the hydrodynamics of the Guadalquivir estuary presents a net upstream transport of passive particles (sediments) in its lower reaches, particularly in spring tides. Larvae hatching in the Gulf of Cadiz (Baldó et al., 2006) are transported eastward by dominant westerlies in the warm season (this dominance varies from year to year [Ruiz et al., 2006]), could be passively “trapped” into the estuary or unless they could effortlessly enter the estuary helped by the general hydrodynamic conditions at the mouth of the Guadalquivir. This hypothesis also needs to be tested.

The results obtained in this study show that the STST hypothesis does not hold for the studied species, at least in the Guadalquivir estuary. The pelagic and benthic behaviour of anchovies and gobies, respectively,

seems to be rather persistent and did not exhibit plasticity under the conditions of the surveys. Anchovies show positive phototropism (Giráldez, 2021) that would tend to maintain them near the surface, due to the strong, turbidity-induced, light attenuation with depth (Ruiz et al., 2017b). As most gobies, *Pomatoschistus* spp., have a visible and large bladder in larvae stages, which reduces in size during its development as an adaptation to its near bed living conditions (Patzner et al., 2011). Thus, any upwards movement is at the expense of active swimming against negative buoyancy. In addition, the ability to detect pressure changes is known in mollusk, crab, barnacle, and fish larvae (Kingsford et al., 2002), and hydrostatic pressure changes associated with tides may guide larvae to maintain their position in the water column despite the current velocities. In fact, in a well-mixed and tidally dominated estuary, such as the Guadalquivir, where the physico-chemical conditions are relatively uniform along the water column, small organisms may be using other alternative strategies to ingress and maintain their position, such as the use of current dynamics at shallower margins.

5. Conclusions

Summarizing, gobies showed upstream flood transport near the bottom, especially near both margins. On the contrary, anchovies showed downstream ebb egress near the surface, although a distribution at the margins of the estuary was observed during the flood tide for larger individuals, showing an influence of ontogenetic stages. Different physicochemical factors were associated with each species distribution in the estuary section studied. Although further research is necessary to better understand the recruitment strategy of these fish species (for example, the influence of neap tides or of the shallowest riverside shores), a first view of distributions was found for each. Furthermore, the present analysis of the distribution across the river helps design appropriate sampling protocols for future study of plankton in estuaries.

CRediT authorship contribution statement

J.M. Miró: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **C. Megina:** Writing – review & editing, Supervision, Methodology. **E. Garel:** Writing – review & editing, Supervision. **I. Donázar-Aramendía:** Methodology, Investigation. **L. Olaya-Ponzone:** Project administration, Methodology, Investigation. **J.C. García-Gómez:** Writing – review & editing, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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