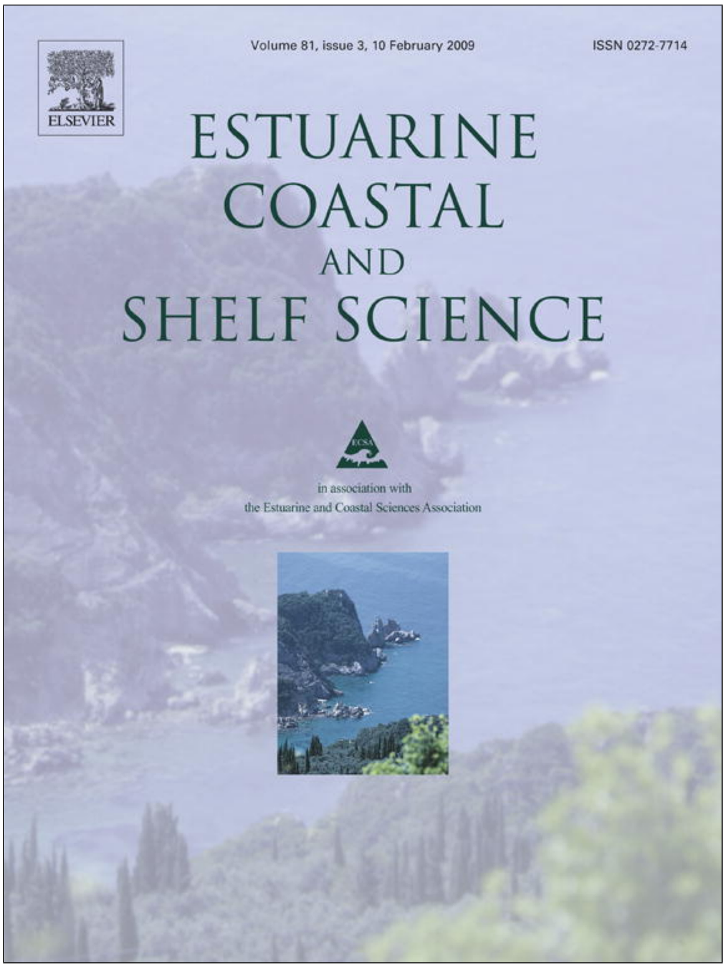
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Small-scale distribution of *Solea solea* and *Solea senegalensis* juveniles in the Tagus estuary (Portugal)

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ABSTRACT

The distribution of *Solea solea* and *Solea senegalensis* in the Tagus estuary was studied following a small-scale approach. Preliminary sampling revealed that sole concentrated in two areas within their nursery grounds, the main subtidal channel and a large intertidal mudflat. Beam trawls were conducted intensively in the two areas in July 2006. Depth, salinity and water temperature were measured. Substrate samples were collected for sediment type determination and macrobenthos identification and quantification. Generalized linear models were applied in order to explain the occurrence and variability of soles' densities, using depth, salinity, water temperature and abundance of polychaetes, oligochaetes, amphipods, isopods and bivalves as explanatory variables. While *S. solea* was more abundant in the main subtidal channel, a deeper, warmer and lower salinity area, *S. senegalensis* abundance was highest at the intertidal mudflat area. Presence of both species in the two areas was associated with abundance of polychaetes (generally with another variable associated), and for *S. senegalensis* in the subtidal channel it was associated with amphipods and depth. Abundance of *S. solea* in the main subtidal channel was associated mainly with polychaetes abundance, while that of *S. senegalensis* was associated with amphipods density. In the intertidal mudflat, bivalves and polychaetes presented significant relationships with both species densities. Some of the factors that had been reported to be important for the distribution of these species in previous studies also do so at a finer scale; however, this small-scale approach provided an in-depth knowledge on habitat selection and spatial segregation of these species within this nursery area.

1. Introduction

The study of habitat use by fish has long been an important subject within fish ecology. Flatfish are among the most studied fish because of their high commercial value. A considerable amount of work has focused on identifying what determines the distribution of juvenile flatfish in nursery areas (e.g. Dorel et al., 1991; Rogers, 1992; Jager et al., 1993; Norcross et al., 1997; Amara et al., 2001; Le Pape et al., 2003; Nicolas et al., 2007), since it is believed that recruitment to the adult stock depends not only on the survival of the eggs and larvae but also on the survival and fitness of the juveniles that concentrate in these areas (Wiens, 1977; Houde, 1989; Beck et al., 2001). Nevertheless, most studies provide only a general picture of habitat use by juvenile fishes in nursery areas, due to the macro-scale sampling strategies employed. In order to better understand the habitat use patterns of fish within nursery areas, a small-scale approach is needed. Baltz et al. (1993) defined microhabitat as the site an individual fish occupies at a given point in time and concluded that careful measurements of many individuals associated with physical, chemical and biological variables should define the response of the population to environmental gradients. Research by Allen and Baltz (1997), Baltz et al. (1998) and Switzer et al. (2004) provided important insights into habitat use at a small-scale by flatfish juveniles in North American estuarine nursery areas. These studies presented crucial information for the understanding of the dynamics of those estuarine nurseries namely regarding species distribution within nursery areas and the variables driving habitat selection. This knowledge is lacking for European nursery areas. Given the importance of the Tagus estuary flatfish community (Cabral et al., 2007), it is of interest to study the habitat use patterns of the two most abundant flatfish species, *Solea solea* and *Solea senegalensis*, within its nursery grounds (Costa and Bruxelas, 1989; Cabral and Costa, 1999; Vinagre and Cabral, 2008; Vinagre et al., 2008). Several studies have produced important information on sole distribution at an estuarine scale throughout Europe, although the majority were conducted in areas where only *S. solea* exists. Most of these studies indicate that higher densities of juvenile sole occur in shallow areas with fine sediment (e.g.

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Koutsikopoulos et al., 1989; Dorel and Desaunay, 1991; Dorel et al., 1991; Rogers, 1992) and low salinity (e.g. Marchand and Masson, 1989; Marchand, 1991). Previous studies in the Tagus estuary have highlighted that juvenile *S. solea* and *S. senegalensis* concentrate in similar conditions to those found in other estuaries (Costa and Bruxelas, 1989; Cabral and Costa, 1999; Vinagre et al., 2006), yet all these studies were based upon macro-scale sampling strategies that did not cover all the habitats within the nursery area and failed to identify the areas of high concentration of these species juveniles on a fine-scale. In the Tagus estuary, juveniles of these species are the main target of beam trawl fisheries, occurring within the nursery areas (Baeta et al., 2005), which renders its management and in-depth knowledge on its habitat use patterns crucial for stocks' protection.

The aim of the present work was to (1) identify the main areas occupied by *Solea solea* and *Solea senegalensis* and (2) to identify the main variables driving their distribution within the estuarine nursery grounds where the two species occur together, using a small-scale approach.

2. Materials and methods

2.1. Study area

The Tagus estuary (Fig. 1), with an area of 325 km^2, is a partially mixed estuary with a tidal range of *ca.* 4 m. This estuarine system has a mean depth less than 10 m and about 40% of its area is intertidal fringed by extensive areas of salt marshes (Caçador et al., 1996). Although its bottom is composed of a heterogeneous assortment of substrates, its prevalent sediment is muddy sand in the upper and middle estuary and sand in the lower estuary and adjoining coastal area (Cabral and Costa, 1999). The mean river flow is 400 m^3 s^{-1}, though it is highly variable both seasonally and inter-annually. Salinity varies from 0, 50-km upstream, to *ca.* 35 at the mouth of the estuary (Cabral et al., 2001). Water temperature ranges from 8 °C to 26 °C (Cabral et al., 2001).

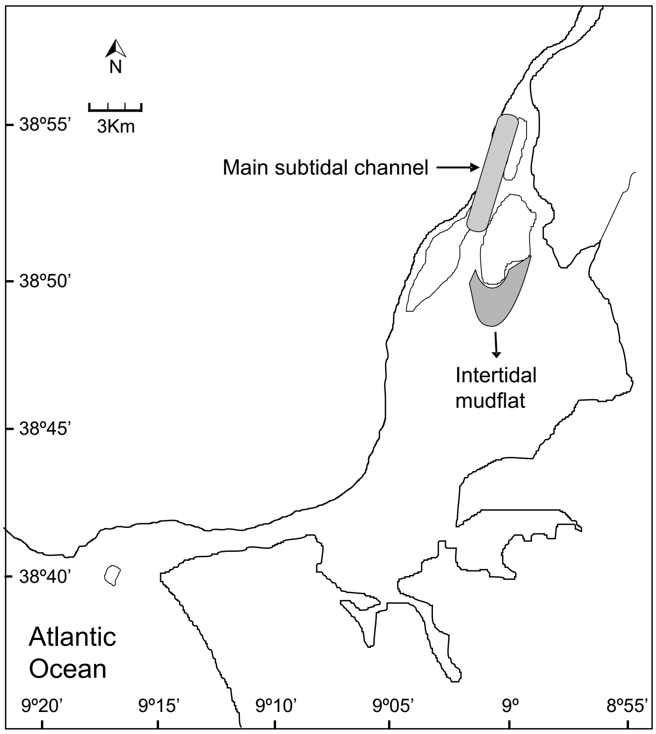

Fig. 1. Location of the main subtidal channel and of the intertidal mudflat area in the Tagus estuary study area.

Two important nurseries for sole have been identified in the Tagus estuary in previous studies by Costa and Bruxelas (1989) and Cabral and Costa (1999), yet only in one of the nursery grounds do the two soles occur together (*Solea solea* only occurs in the uppermost nursery area, near Vila Franca de Xira), and is thus the focus of this study. This nursery has a mean depth of 4.4 m, and has low and highly variable salinity and a high proportion of fine sand in the substrate (Cabral and Costa, 1999). *Solea solea* 0-group juveniles are known to colonise this nursery around May leaving the estuary towards the coast in October–November (Cabral and Costa, 1999). *Solea senegalensis* colonise the upper Tagus later, yet in July high abundance of both species can be found at this nursery (Cabral and Costa, 1999).

2.2. Sampling

Beam trawls were conducted in this nursery in July 2006 in order to capture *Solea solea* and *Solea senegalensis*. Preliminary sampling, random by habitat type, was carried out in all the channels and around the estuarine islands of the nursery in order to determine where soles were concentrated. It was concluded that both species concentrated in two areas, the main subtidal channel and a broad intertidal mudflat (Fig. 1). This approach was useful since it allowed us to concentrate the sampling effort in the areas where soles concentrate. An intensive sampling program was implemented in these two areas in order to study the distribution of soles in a small-scale. A total of 84 hauls were conducted randomly within both these areas (58 hauls in the main channel and 26 in the intertidal mudflat area). A minimum distance of 10 m was kept between trawls during each sampling session, in order to prevent running over areas already disturbed by the fishing gear. The average area swept by each trawl was 1088 m^{-2}. We estimate that density of trawls was 23.77 trawls 1000 m^{-2} in the main channel and 16.25 trawls 1000 m^{-2} in the mudflat, over the whole sampling period. Trawls were conducted with a 2-m beam trawl with 5-mm stretched mesh at the cod end. The length of the average tow was 544 m. All soles caught were identified. Although these species are very similar, they can be easily distinguished in the field through close inspection of the pectoral fin of the ocular side, which presents different coloration. The distance travelled in each tow was determined based on a global positioning system device (GPS) and the headline length was used as a measure of width in the swept area calculations. Fish abundance was expressed as density (number of individuals per 1000 m^2). Mean density and standard deviation per area were calculated. Depth, temperature and salinity were measured at the beginning of each trawl. At the beginning of each trawl, and at every 100 m, a sediment sample was taken with a van Veen grab, for macrobenthic organisms' collection. Another sediment sample was taken for sediment type assessment. Sediments were transported to the laboratory and then sieved through a 0.5-mm nylon mesh to collect specimens. Organisms were preserved in 4% buffered formalin and identified at a later date. Polychaetes, amphipods, isopods, bivalves and oligochaetes' densities were selected as variables for analyses since they were composed mainly of *S. solea* and *S. senegalensis* prey. Sediment samples were dried at 60 °C and a 100 g subsample was wet-sieved through a 0.063-mm mesh sieve and dried. The remaining sediment was sieved through a four-sieve column. Weight of the residue remaining in each sieve was then expressed as a percentage of the total subsample weight and the <0.063-mm fraction calculated from the difference between the initial subsample weight and the sum of the other fractions. The following categories of grain size were considered: mud (<0.063 mm), fine sand (0.063–0.125 mm), medium sand (0.125–0.500 mm), coarse sand (0.500–2 mm) and gravel (>2 mm).

2.3. Data analyses

Data were pair plotted in order to investigate multi-colinearity between the independent variables. The variables used in the GLM models did not present multi-colinearity. Whenever multi-colinearity was detected, the variable known to have a more direct influence over these species distribution was maintained, while the other variable, or variables, was eliminated from the analysis. Observation of frequency distributions for both sole species densities revealed high positive skewness with a considerable proportion of zero catch. In order to account for both the probability of occurrence and the variation of abundance at each sampling station, modelling was conducted in two steps: (1) estimation of the probability of presence of the fish and (2) estimation of abundance conditional to positive catch.

The first step was modelled through a Logistic regression model with a logit link (Hosmer and Lemeshow, 1989), while the second step was modelled by a Gamma regression model with a log link (McCullagh and Nelder, 1989).

The goodness-of-fit of the models was assessed by comparing their relative contribution to total deviance explained. Statistical analyses were performed using R software (R Development Core Team, 2005). A significance level of 0.05 was considered in all test procedures.

3. Results

Solea solea mean size was 95 mm, while that of *Solea senegalensis* was 94 mm. While *S. solea* was more abundant in the main subtidal channel, *S. senegalensis* density was highest in the intertidal mudflat area. The mean density of *S. solea* in the main subtidal channel was 6.04 ind. 1000 m^{-2}, while in the intertidal mudflat area it was 0.42 ind. 1000 m^{-2}. *Solea senegalensis's* density in the main subtidal channel was 0.73 ind. 1000 m^{-2}, while in the intertidal mudflat area it was 3.09 ind. 1000 m^{-2}. The main channel area was on average deeper and had lower salinity and higher temperatures than the intertidal mudflat area (Table 1). The main subtidal channel had higher density of polychaetes and amphipods than the intertidal mudflat area, while the mudflat intertidal area had higher densities of oligochaetes and much higher densities of bivalves and isopods than the main subtidal channel (Table 1). The main subtidal channel substrate was composed of fine sand, while that of the intertidal mudflat was composed of mud.

Generalized linear models revealed that the occurrence of both species in both areas was associated with the abundance of polychaetes (usually associated with another variable). *Solea senegalensis* in the main subtidal channel was, however, also associated with abundance of amphipods and depth (Table 2). Abundance of *Solea solea* in the main channel was associated mainly with polychaetes and salinity and also, to a lesser degree, with depth, isopods and bivalves, as well as, with interactions among some of these variables (Table 2). Abundance of *S. senegalensis* in the main subtidal channel was associated mainly with amphipods and, to a lesser degree, with depth (Table 2). Abundance of *S. solea* in the intertidal mudflat was associated mainly with polychaetes, bivalves and isopods, and to a lesser degree with depth, oligochaetes and salinity (Table 3). Abundance of *S. senegalensis* in the intertidal mudflat area was associated mainly with bivalves and polychaetes and, to a lesser degree, with depth, temperature, salinity, isopods, oligochaetes, as well as, with interactions among some of these variables (Table 3). With the exception of the Logistic model for *S. senegalensis* in the main subtidal channel, all models presented high explanatory levels.

Table 2
Goodness-of-fit statistics for the Logistic and Gamma regression models fitted to both species densities in the main channel (values of deviance for each factor, residual deviance (Res. Dev.), deviance, percentage of the total deviance explained by each factor (% Expl.), and *p* values are presented).

Predictor	*p* value	Res. Dev.	Deviance	% Expl.
Logistic model				
S. solea				
NULL		23.613		
Main effects				
Polychaetes	0.050	7.403	16.210	68.650
Total explained				68.650
S. senegalensis				
NULL		76.992		
Main effects				
Amphipods	0.020	70.073	6.919	8.987
Depth	0.039	67.686	9.306	3.100
Total explained				12.087
Gamma model				
S. solea				
NULL		57.834		
Main effects				
Polychaetes	<0.001	27.552	30.282	52.360
Isopods	0.048	24.928	32.906	4.537
Bivalves	0.040	24.728	33.106	0.346
Salinity	<0.001	14.227	43.607	18.157
Depth	<0.001	10.708	47.126	6.085
Interactions				
Polychaetes:Bivalves	0.023	10.303	47.531	0.700
Polychaetes:Salinity	0.008	9.802	48.032	0.866
Polychaetes:Depth	0.001	9.014	48.820	1.363
Salinity:Depth	0.004	8.297	49.537	1.240
Total explained				85.654
S. senegalensis				
NULL		34.759		
Main effects				
Amphipods	<0.001	5.513	29.246	84.139
Depth	0.007	5.414	29.345	0.285
Total explained				84.424

4. Discussion

The small-scale sampling approach revealed that *Solea solea* and *Solea senegalensis* exploit the nursery habitat in different ways;

Table 1
Mean values (and standard deviations in parentheses) of the environmental variables and prey abundance in the main channel and in the intertidal mudflat.

	Depth (m)	Salinity	Temperature (°C)	Polychaeta (ind. m^{-2})	Oligochaeta (ind. m^{-2})	Amphipoda (ind. m^{-2})	Isopoda (ind. m^{-2})	Bivalvia (ind. m^{-2})
Main channel	5.20 (1.17)	2.39 (2.83)	23.69 (3.59)	191.18 (92.83)	65.89 (150.40)	55.93 (83.23)	21.48 (42.54)	4.35 (15.71)
Intertidal mudflat	3.35 (1.81)	14.37 (3.46)	20.77 (1.10)	111.18 (169.32)	197.93 (281.74)	19.56 (22.37)	671.56 (690.35)	304.07 (365.22)

Table 3
Goodness-of-fit statistics for the Logistic and Gamma regression models fitted to both species densities in the intertidal mudflat area (values of deviance for each factor, residual deviance (Res. Dev.), deviance, percentage of the total deviance explained by each factor (% Expl.), and *p* values are presented).

Predictor	*p* value	Res. Dev.	Deviance	% Expl.
Logistic model				
S. solea				
NULL		38.673		
Main effects				
Polychaeta	0.006	15.903	22.770	58.878
Oligochaeta	0.030	10.560	28.113	13.816
Total explained				72.694
S. senegalensis				
NULL		36.498		
Main effects				
Polychaeta	0.017	18.300	18.198	49.860
Depth	0.006	5.682	30.816	34.621
Total explained				84.481
Gamma model				
S. solea				
NULL		5.065		
Main effects				
Polychaeta	0.003	2.113	2.952	58.278
Isopoda	0.047	1.451	3.614	13.081
Oligochaeta	<0.001	1.362	3.703	1.759
Bivalvia	<0.001	0.498	4.568	17.061
Salinity	<0.001	0.306	4.759	0.163
Depth	<0.001	0.314	4.751	3.613
Total explained				93.955
S. senegalensis				
NULL		15.334		
Main effects				
Polychaeta	0.001	9.992	5.342	34.836
Isopoda	0.024	9.632	5.703	2.352
Oligochaeta	0.004	9.408	5.926	1.457
Bivalvia	0.001	3.175	12.159	40.648
Depth	<0.001	2.386	12.949	5.150
Salinity	<0.001	1.994	13.341	2.556
Temperature	<0.001	1.186	14.148	5.263
Interactions				
Isopoda:Salinity	0.008	0.921	14.414	1.734
Oligochaeta:Temperature	0.027	0.915	14.419	0.033
Bivalvia:Salinity	0.022	0.898	14.436	0.114
Salinity:Temperature	0.027	0.176	15.158	4.710
Total explained				98.853

S. solea concentrate in the main subtidal channel, a deeper area with fine sand substrate and low salinity, while *S. senegalensis* concentrate in a downstream large intertidal mudflat. Allen and Baltz (1997) and Switzer et al. (2004) also reported spatial segregation of flatfish species within nursery areas in North America and referred various associations of abiotic variables as important factors influencing the abundance of the different species. Several experimental studies also showed that different species of flatfishes have different sediment preferences (Moles and Norcross, 1995; Stoner and Ottmar, 2003; Stoner and Titgen, 2003). Yet, to the best of our knowledge, all previous studies that examined flatfish habitat use on a fine-scale investigated only abiotic variables, not taking into account biotic variables, such as abundance of prey, meaning that the present study was the first to examine the effect of these important variables at this scale.

The present study revealed the importance of polychaetes in the occurrence and abundance of both soles, regardless of habitat type. The exception of *S. senegalensis* in the main subtidal channel, which was associated with amphipods and slightly deeper depth, can be explained by the low densities of *S. senegalensis* in this area. The low numbers of *S. senegalensis* may not allow them to explore the entire range of optimum habitat. It should be noted that the explanatory percentage of the Logistic model is low in this case.

In the mudflat area, bivalve density was also a very important factor influencing the densities of both species. Since both soles responded in similar ways to prey abundance and type (albeit with small differences in associated variables with lower explanatory levels), it seems that the spatial segregation that occurred within the nursery is based on abiotic factors.

Cabral and Costa (1999) using a macro-scale approach that analysed the whole upper Tagus estuary, concluded that *Solea solea* concentrated in deeper, warmer, lower salinity areas, with fine sand and high densities of amphipods. The same study concluded that for *Solea senegalensis* only density of polychaetes and bivalves were significant factors explaining density.

The present small-scale analysis confirmed some of the conclusions of the previous macro-scale study by Cabral and Costa (1999), providing also more detailed information on the area where both sole species occur together, revealing that some of the factors that influence the distribution and abundance of these species on a macro-scale, also do so at a finer scale, especially concerning the main abiotic factors identified for *Solea solea*.

It is interesting to notice that some differences in explanatory variables among species detected by Cabral and Costa (1999) appear to be due to habitat type when examined at a smaller scale. The only variables found to have significant relations with *Solea senegalensis* densities, on a macro-scale, were polychaetes and bivalves probably because this species concentrate in intertidal mudflats rich in these prey. Thus, some of the relations found on a macro-scale probably occurred because of the differential abundance of each prey species according to substrate. These authors also reported that the abundance of bivalves and polychaetes was not important for *Solea solea* densities. At a fine-scale it was concluded that these factors present significant relations with the densities of both soles in the mudflat area.

In the Cabral and Costa (1999) study polychaetes were found to be an important factor only for *Solea senegalensis*, while amphipods were the only important prey influencing *Solea solea* densities. In the present study, amphipods were found to be important only for *S. senegalensis*, and only in the main channel area, where this species abundance was scarce, while polychaetes seem to be very important for *S. solea* in both areas and for *S. senegalensis* in the intertidal mudflat. Soles are known to be generalist and opportunistic foragers that can switch prey items in accordance with food availability. This could explain distribution according to fluctuations in the densities of the macrobenthic organisms, meaning that inter-annual variability in biota densities may have played an important role in the results obtained. Thus, in years when recruitment of amphipods is very successful leading to higher availability of this prey it may be an important factor for soles densities, since the feeding behaviour of these species is quite flexible (e.g. Lagardère, 1987; Molinero et al., 1991; Henderson et al., 1992; Cabral, 2000).

Habitat selection is generally assumed to be driven by species resource requirements (Hurlbert, 1981). In the context of fish nurseries, habitat availability and selection will influence the relative fitness and growth attained by individuals by the end of the nursery period, thus determining recruitment to the adult population (Sogard, 1994; Beck et al., 2001). The present work highlights the importance of habitat diversity for nurseries ability to sustain various species of juveniles.

5. Conclusions

In conclusion, *Solea solea* and *Solea senegalensis* juveniles are trophic generalists that can explore different habitats and prey items within a nursery area, however, they display preferences, mainly regarding abiotic conditions that lead to some spatial segregation. Mudflats seem to be especially important for *S. senegalensis*. Potential loss of these intertidal areas due to the sea level rise predicted by climate change models (Miranda et al., 2002) should be an issue of concern. Knowledge on the fine-scale distribution of juvenile soles should be taken into account in future management of these areas, since these are the most important species of commercial value using these areas as nurseries.

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