



## Nursery use patterns of commercially important marine fish species in estuarine systems along the Portuguese coast

R.P. Vasconcelos<sup>a,\*</sup>, P. Reis-Santos<sup>a</sup>, A. Maia<sup>a,1</sup>, V. Fonseca<sup>a</sup>, S. França<sup>a</sup>, N. Wouters<sup>a</sup>, M.J. Costa<sup>a,b</sup>, H.N. Cabral<sup>a,b</sup>

<sup>a</sup> Instituto de Oceanografia, Faculdade de Ciências da Universidade de Lisboa, Campo Grande, 1749-016 Lisboa

<sup>b</sup> Departamento de Biologia Animal, Faculdade de Ciências da Universidade de Lisboa, Campo Grande, 1749-016 Lisboa

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### ABSTRACT

Analysing the estuarine use patterns of juveniles of marine migrant fish species is vital for identifying important sites for juveniles as well as the basic environmental features that characterize these sites for different species. This is a key aspect towards understanding nursery function. Various estuarine systems along the Portuguese coast (Minho, Douro, Ria de Aveiro, Mondego, Tejo, Sado, Mira, Ria Formosa and Guadiana) were sampled during Spring and Summer 2005 and 2006. Juveniles of commercially important marine fish species *Solea solea*, *Solea senegalensis*, *Platichthys flesus*, *Diplodus vulgaris* and *Dicentrarchus labrax*, predominantly 0-group individuals, were amongst the most abundant species and had distinct patterns of estuarine use as well as conspicuous associations with several environmental features. Juvenile occurrence and density varied amongst estuaries and sites within them, and differed with species. Sites with consistently high juvenile densities were identified as important juvenile sites (i.e. putative nursery grounds). Through generalized linear models (GLM), intra-estuarine variation in occurrence and density of each of the individual species was largely explained by environmental variables (temperature; salinity; depth; percentage of mud in the sediment; presence of seagrass; importance of intertidal areas; relative distance to estuary mouth; macrozoobenthos densities; and latitude). Decisive environmental factors defining important sites for juveniles varied depending on the system as a result of different environmental gradients, though there were common dominant features for each species regardless of the estuary considered. Analysed environmental variables in the GLM also accounted for inter-estuarine variation in species' occurrence and density. In several estuaries, the identified important juvenile sites were used by many of these species simultaneously and may be of increased value to both management and conservation. Overall, the variability in site features amongst estuaries highlighted the tolerance of these species to different available environmental conditions and provided fundamental information for future spatially explicit modelling of their distribution. This should ultimately enable the prediction of species response to habitat alterations.

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### 1. Introduction

Estuaries and coastal areas are commonly acknowledged as highly productive and valuable ecosystems which provide numerous habitats for fish and support fundamental ecological links with other environments (Costanza et al., 1997; Beck et al.,

2001; Able, 2005). Fish species occupy estuaries permanently (estuarine species), transitionally (anadromous and catadromous), occasionally (freshwater and marine straggler) or during particular life periods, as is the case of marine migrant juveniles which find suitable nursery grounds in estuaries (Franco et al., 2008). The latter have spatially segregated adult and juvenile life stages: adults live in the marine environment and spawn offshore, larvae are transported towards the coast and post-larvae or early juveniles enter and settle in reputed nursery areas such as shallow coastal zones or estuaries (e.g. Koutsikopoulos et al., 1989). Juveniles inhabit these estuaries, generally throughout Spring and Summer, benefiting from suitable conditions for growth, namely high food availability, water temperature and low biotic stress (Blaber and Blaber, 1980; Haedrich, 1983; Miller et al., 1985; Gibson, 1994; Beck

\* Corresponding author.

E-mail addresses: [rpvasconcelos@fc.ul.pt](mailto:rpvasconcelos@fc.ul.pt) (R.P. Vasconcelos), [pnsantos@fc.ul.pt](mailto:pnsantos@fc.ul.pt) (P. Reis-Santos), [amaia@mail.uri.edu](mailto:amaia@mail.uri.edu) (A. Maia), [vffonseca@fc.ul.pt](mailto:vffonseca@fc.ul.pt) (V. Fonseca), [sofranca@fc.ul.pt](mailto:sofranca@fc.ul.pt) (S. França), [nwouters@fc.ul.pt](mailto:nwouters@fc.ul.pt) (N. Wouters), [mjcosta@fc.ul.pt](mailto:mjcosta@fc.ul.pt) (M.J. Costa), [hcabral@fc.ul.pt](mailto:hcabral@fc.ul.pt) (H.N. Cabral).

<sup>1</sup> Present address: Department of Biological Sciences, 100 Flagg Road, University of Rhode Island, Kingston, RI 02881-0816, USA

et al., 2001), though with some associated physiological cost due to natural (e.g. salinity dynamics) or artificial stressors (e.g. pollution) (Yamashita et al., 2003; Amara et al., 2007), until recruiting to adult subpopulations in the marine environment.

Along the Portuguese coast several estuaries have been suggested as important putative nursery areas for commercially important marine fish species, namely the flatfishes common sole *Solea solea*, Senegalese sole *Solea senegalensis* and flounder *Platichthys flesus* and the perciformes common two-banded sea bream *Diplodus vulgaris* and sea bass *Dicentrarchus labrax* (e.g. Cabral and Costa, 1999; Pombo et al., 2002; Veiga et al., 2006; Cabral et al., 2007; Martinho et al., 2007). Adults of these species inhabit the coast and continental shelf and are among the most valuable marine fishes captured in Portuguese fisheries, mainly in multi-species fisheries as trammel nets and longline. Overall total annual landings of these five species represent ca. 14.0% of transactions in value, although they only account for 2.2% in weight (Instituto Nacional de Estatística, 2009).

The distribution of juveniles of marine migrant species within estuarine grounds and their use of particular areas results from the responses of individuals to multiple environmental variables, which can be either highly dynamic (e.g. salinity, water temperature, food availability) or fairly stable (e.g. sediment type, presence of seagrass) (Stoner et al., 2001; Selleslagh et al., 2009). Estuarine use patterns by juvenile fish have mostly been characterized for single estuaries and individual species, including *S. solea*, *P. flesus* and *D. labrax* in distinct estuaries (e.g. Kelley, 1988; Kerstan, 1991; Marchand, 1991; Cabral and Costa, 1999, 2001; Freitas et al., 2009). However, such results represent a small part of the species overall scenarios of environmental use patterns and of their tolerance to different conditions, particularly since the degree to which species use different estuaries appears to vary both among and within estuaries (Able and Grothues, 2007). Therefore, multi-estuary approaches provide enhanced evidence of species estuarine use and enable direct comparison of arising patterns (Goldberg et al., 2002; Le Pape et al., 2003a; Lazzari, 2008; Selleslagh et al., 2009). Analysing estuarine use patterns by juveniles in a set of closely located estuaries should indicate the factors that define juvenile fish occurrence and density in estuarine sites. Moreover, it should clarify the influence of such factors to the variation in the nursery function of different sites and estuaries.

The present study analysed the estuarine use patterns of juvenile *S. solea*, *S. senegalensis*, *P. flesus*, *D. vulgaris* and *D. labrax* in nine main estuarine systems of the Portuguese coast. Specifically, it addressed if each species' occurrence and density differed amongst estuaries and sites within them and if particular sites or estuaries could be highlighted as important sites for juveniles and, therefore, potential nursery areas. Moreover, by modelling the response of juvenile occurrence and density to the environmental variables of these sites, this study aimed to identify which variables best explained intra- and inter-estuarine variability in juvenile distribution, and how strongly, in order to characterize the features which define important sites for juveniles of the five species and how these varied amongst systems. The variability or similarity of structuring features amongst the different estuaries illustrate species' tolerance to available nursery conditions and should provide valuable information towards future spatially explicit predictions of species' distribution responses and resilience to potential changes in estuarine conditions. Furthermore, variability of spatial and environmental use patterns amongst estuarine areas should provide knowledge on the relevance of local regulation in defining nursery function. Ultimately, identifying important sites for juveniles represents a fundamental step towards the accurate definition of estuarine nursery areas (sensu Beck et al., 2001) essential for these species metapopulations.

## 2. Material and methods

### 2.1. Study area

Nine estuarine systems along the Portuguese coast were selected for their potential or acknowledged importance as putative fish nursery areas: Minho, Douro, Ria de Aveiro, Mondego, Tejo, Sado, Mira, Ria Formosa and Guadiana (Fig. 1) (e.g. Cabral and Costa, 1999; Pombo et al., 2002; Veiga et al., 2006; Cabral et al., 2007; Martinho et al., 2007). These systems differ in their hydrological and geomorphological features, as well as in the level and type of anthropogenic pressures they are subject to (see Vasconcelos et al., 2007).

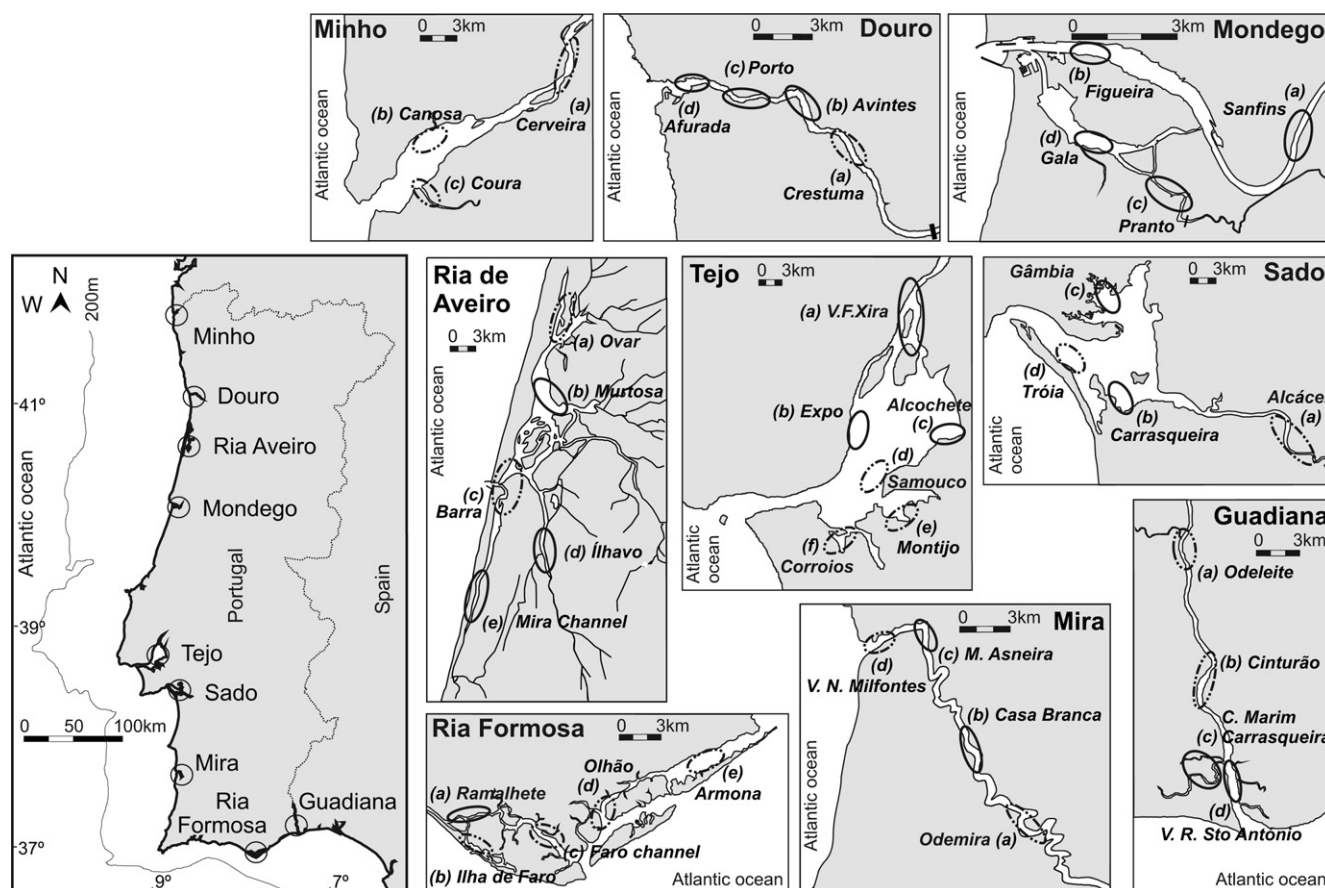
### 2.2. Sampling surveys

Fishing surveys were carried out in Spring (May) and Summer (July) of two consecutive years (2005 and 2006). May follows the start of estuarine colonization of many marine migrant species into the estuaries along this coast, particularly *S. solea*, *S. senegalensis*, *P. flesus* and *D. labrax* (Cabral and Costa, 1999, 2001; Dolbeth et al., 2008). To avoid temporal variations in each season, surveys were conducted in the shortest time frame possible (a fortnight). Sampling sites in each system were defined based on previous knowledge and on preliminary surveys. In 2005, juveniles were sampled in the main areas where their occurrence had been previously described; whilst in 2006, fish sampling was also carried out in additional sites throughout the entire estuaries (Fig. 1). The Minho estuary was only sampled in 2006.

Sampling took place during the night using a beam trawl (2 m wide beam, tickler chain, net with 5 mm mesh in the cod end). The selected fishing gear efficiently samples the benthic-demersal assemblage (Hemingway and Elliott, 2002; Leitão et al., 2007) and is commonly used in studies targeting juveniles of these species (Cabral and Costa, 2001; Le Pape et al., 2003a; Martinho et al., 2007; Cabral et al., 2007). Tow location and distance were determined with a GPS. Ten replicate tows were made per site and season during ebb tide (tow duration ca. 10 min; mean speed  $0.8 \text{ m s}^{-1}$ ; mean area  $862 \text{ m}^2$ ). Upon collection, fish were stored and transported on ice to the laboratory and preserved frozen. Subsequently, individual fish length was determined (total length  $L_t$ , measured to the nearest mm).

Simultaneously with fish sampling, site environmental characteristics were determined in each tow, namely: water temperature and salinity (using a multi-parameter probe), depth and presence/absence of submersed aquatic vegetation, such as seagrass. In each estuarine site, three replicate sediment samples were collected with a modified van Veen grab ( $0.05 \text{ m}^2$ ) for the determination of mean percentage of mud in the sediment (percentage of dry sediment not retained in a  $0.063 \text{ mm}$  calibrated sieve); and additional three replicate samples for determination of the mean density of three abundant taxonomic groups of macrozoobenthos (individuals retained in a  $0.5 \text{ mm}$  calibrated sieve) – Annelida, Arthropoda and Mollusca. As these groups constitute the main prey for juveniles of the presently analysed fish species (see summary in Reis-Santos et al., 2008), their density represents an adequate measure of prey availability (Stoner et al., 2001; Nicolas et al., 2007).

Additional characteristics of each estuarine site were subsequently determined, based on in situ observation, aerial photographs, nautical charts and GIS software, namely: importance of intertidal areas (classified as: negligible, narrow banks, wide banks and some flats, extensive flats, or total; according to the proportion of intertidal areas, respectively 0%, 25%, 50%, 75% or 100%) and relative distance to the estuary mouth (from 0 at the estuary mouth to 1 at the most distant site) (Table 1).



**Fig. 1.** Sampled estuarine systems along the Portuguese coast: Minho, Douro, Ria de Aveiro, Mondego, Tejo, Sado, Mira, Ria Formosa and Guadiana. Also shown is the location of sampled sites within each estuary (three to six sites were sampled per estuary and are marked as "a, b, c, d and e"); sites sampled in both 2005 and 2006 are represented with full line ellipses (○) and sites sampled only in 2006 with broken line ellipses (⋯).

### 2.3. Data analysis

Fish species' densities were determined and expressed in individuals  $1000 \text{ m}^{-2}$  for each tow. Mean (and standard error) densities of each species per estuarine site and season were determined for 2005 and 2006. The most frequent, abundant and commercially important marine migrant species were selected as model species for all subsequent analysis, specifically *S. solea*, *S. senegalensis*, *P. flesus*, *D. vulgaris* and *D. labrax*.

Length frequency distributions (in 10 mm length intervals) of each species were plotted for each estuarine site and season, for 2005 and 2006 data.

Variation in species' density per estuarine site and season were plotted for both 2005 and 2006 data. Univariate statistics were used to explore species spatial distributions, i.e. estuary and site within an estuary as independent factors. Since raw and transformed data failed the assumptions of normality and homoscedasticity parametric tests could not be used. For each species, the non-parametric test Kruskal–Wallis was used to detect differences in density among estuaries (mean density of each site in a season was used as a sample,  $n = 116$ ). Post-hoc comparison Dunn test was applied to detect significant differences between pairs of groups. For each species and estuary a Kruskal–Wallis test was performed to test intra-estuarine differences in densities.

In each estuary, sites with consistently high juvenile densities amongst all sampling periods were identified as important sites for juveniles of each species. The total area of these sites was determined with GIS software, as a measure of habitat quantity in these systems.

Generalized linear models (GLM) were conducted in R software (R Development Core Team, 2005), using the 2006 data, to investigate the response of each species distribution to predictor environmental variables. GLM are an extension of linear models which allow the incorporation of non-normal distributions of the response variable and transformations of the dependent variables to linearity (McCullagh and Nelder, 1989). The GLM approach was applied to extract environmental features associated with estuarine use patterns (significant parameters with high percentage of explained data variability), evaluate if they are similar amongst estuaries and identify the fundamental features which define important sites for juveniles of a particular species. Considering known and expected spatial differences in species distribution within an estuary, distributions of these five species were analysed separately. Moreover, each species distribution was modelled both in individual estuaries and in all estuaries collectively to address the variables related to its intra- and inter-estuarine variability, respectively. Predictor variables considered in the models are listed in Table 1. Each tow corresponded to a sample in the analysis. Due to the abundance of null values in the response variable species density, the applied GLM consisted of a delta approach and included two models estimating: (1) the probability of species presence ( $P_{0/1}$ ), through a binomial law, i.e. logistic regression, with a logit link function; (2) species density (*Dens*) through a Gamma distribution with a log link function, after excluding cases with null values of the response variable. A significance level of  $P < 0.05$  was considered in all GLM procedures. Percentage of total deviance explained and relative contribution of each factor were evaluated for each model. Since macrozoobenthos data was not available for

**Table 1**

Environmental features (mean values for May and July 2005 and 2006) in sites sampled in estuarine systems along the Portuguese coast (Min – Minho, D – Douro, RA – Ria de Aveiro, Mo – Mondego, T – Tejo, S – Sado, Mir – Mira, RF – Ria Formosa, G – Guadiana): tem – water temperature (°C); sal – salinity; dep – depth (m); mud – percentage of mud in the sediment (% dry weight); sea – seagrass (0 – absence, 1 – presence); int – importance of intertidal areas (classified as: negligible, narrow banks, wide banks and some flats, extensive flats, or total; according to the proportion of intertidal areas, respectively 0%, 25%, 50%, 75% or 100%); dis – relative distance to the estuary mouth (from 0 at the estuary mouth to 1 at the most distant site); lat – latitude at estuary mouth (°N); ann – annelida density, art – arthropoda density, mol – mollusca density, ben – density of the three macrozoobenthos groups (individuals m<sup>2</sup>).

Estuary	Site	Tem (°C)	Sal	Dep (m)	Mud (% dw/dw)	Sea (0/1)	Int (0–100%)	Dis (0–1)	Lat (°N)	Ann	Art	Mol	Ben
										(individuals m <sup>2</sup> )			
Min	a	20.01	0.04	4.05	14.20	0	0	1.00	41.9	480	1180	0	1660
	b	17.55	19.14	2.49	7.79	0	50	0.36	41.9	700	220	40	960
	c	17.91	19.20	2.15	20.04	0	50	0.24	41.9	1660	120	0	1780
D	a	20.86	4.29	7.25	0.46	0	0	1.00	41.1	520	80	0	600
	b	20.58	6.58	9.13	0.42	0	0	0.69	41.1	2610	290	10	2910
	c	19.42	10.36	11.58	23.93	0	0	0.43	41.1	3720	310	590	4620
RA	d	18.54	14.92	4.83	31.59	0	0	0.19	41.1	5740	780	720	7240
	a	22.79	26.61	2.19	46.78	0	75	1.00	40.6	470	100	80	650
	b	19.79	32.66	1.84	81.57	0	50	0.55	40.6	825	25	2925	3775
	c	20.72	30.33	2.29	9.63	0	50	0.22	40.6	500	33	400	933
	d	21.89	31.17	2.10	49.50	0	50	0.58	40.6	6318	190	216	4554
	e	24.24	20.90	1.13	59.87	0	50	0.69	40.6	12,167	280	567	13,013
Mo	a	21.45	8.28	3.50	0.78	0	0	1.00	40.1	607	2560	2247	5413
	b	18.33	25.44	3.13	1.34	0	25	0.26	40.1	120	0	100	220
	c	22.96	18.35	1.39	97.61	0	25	0.63	40.1	9670	105	935	10,710
	d	20.04	26.90	1.25	3.00	0	50	0.37	40.1	240	20	1820	2080
	a	22.18	8.32	3.98	60.47	0	75	1.00	38.7	405	310	129	844
	b	21.49	29.27	2.40	67.72	0	75	0.57	38.7	80	195	30	305
	c	22.82	23.52	1.05	97.87	0	75	0.79	38.7	800	3	23	825
	d	19.83	29.85	2.90	60.00	0	75	0.56	38.7	20	0	0	20
	e	24.83	30.53	1.55	80.00	0	75	0.61	38.7	800	3	23	825
	f	23.92	30.19	2.02	80.00	0	75	0.50	38.7	800	3	23	825
S	a	24.31	10.44	1.95	57.49	0	25	1.00	38.5	347	20	0	367
	b	23.92	35.46	1.73	38.14	0	75	0.39	38.5	393	480	260	1133
	c	23.16	36.68	1.15	60.07	0	75	0.54	38.5	170	110	310	590
	d	23.21	35.68	2.54	30.54	0	25	0.23	38.5	40	550	670	1260
Mir	a	24.36	3.98	3.65	70.42	0	25	1.00	37.7	1680	30,893	0	32,573
	b	23.64	19.59	4.31	86.55	0	25	0.72	37.7	1302	1776	400	3478
	c	20.06	33.88	3.05	63.42	1	50	0.15	37.7	11,487	367	5780	17,633
	d	17.78	34.16	3.00	66.81	0	25	0.05	37.7	23,867	1467	5260	30,593
RF	a	23.32	35.71	2.28	30.00	1	75	0.46	37.0	–	–	–	–
	b	22.71	36.43	3.18	0.00	0	75	0.19	37.0	–	–	–	–
	c	23.03	36.27	2.77	0.00	1	75	0.54	37.0	–	–	–	–
	d	23.64	36.03	2.10	88.00	1	75	1.00	37.0	–	–	–	–
	e	24.56	36.27	2.94	88.00	0	75	0.92	37.0	–	–	–	–
G	a	25.35	4.72	4.61	80.54	0	25	1.00	37.2	540	40	0	580
	b	24.81	13.54	4.83	31.77	0	25	0.52	37.2	1790	30	10	1830
	c	23.09	29.49	2.27	74.49	0	50	0.29	37.2	2630	247	253	3130
	d	22.86	26.56	2.45	92.77	0	25	0.25	37.2	580	520	20	1120

Ria Formosa, and only *D. vulgaris* was found in this system, the GLM analysis for inter-estuarine variations of the remaining fish species were performed excluding Ria Formosa; whilst GLM analysis for inter-estuarine variations of *D. vulgaris* were performed excluding this predictor.

### 3. Results

A total of 71 fish species were caught in the nine estuarine systems although density was dominated by only a few. Marine migrants *S. solea*, *S. senegalensis*, *P. flesus*, *D. vulgaris* and *D. labrax* were present in several estuaries and overall amongst the 20 most abundant species.

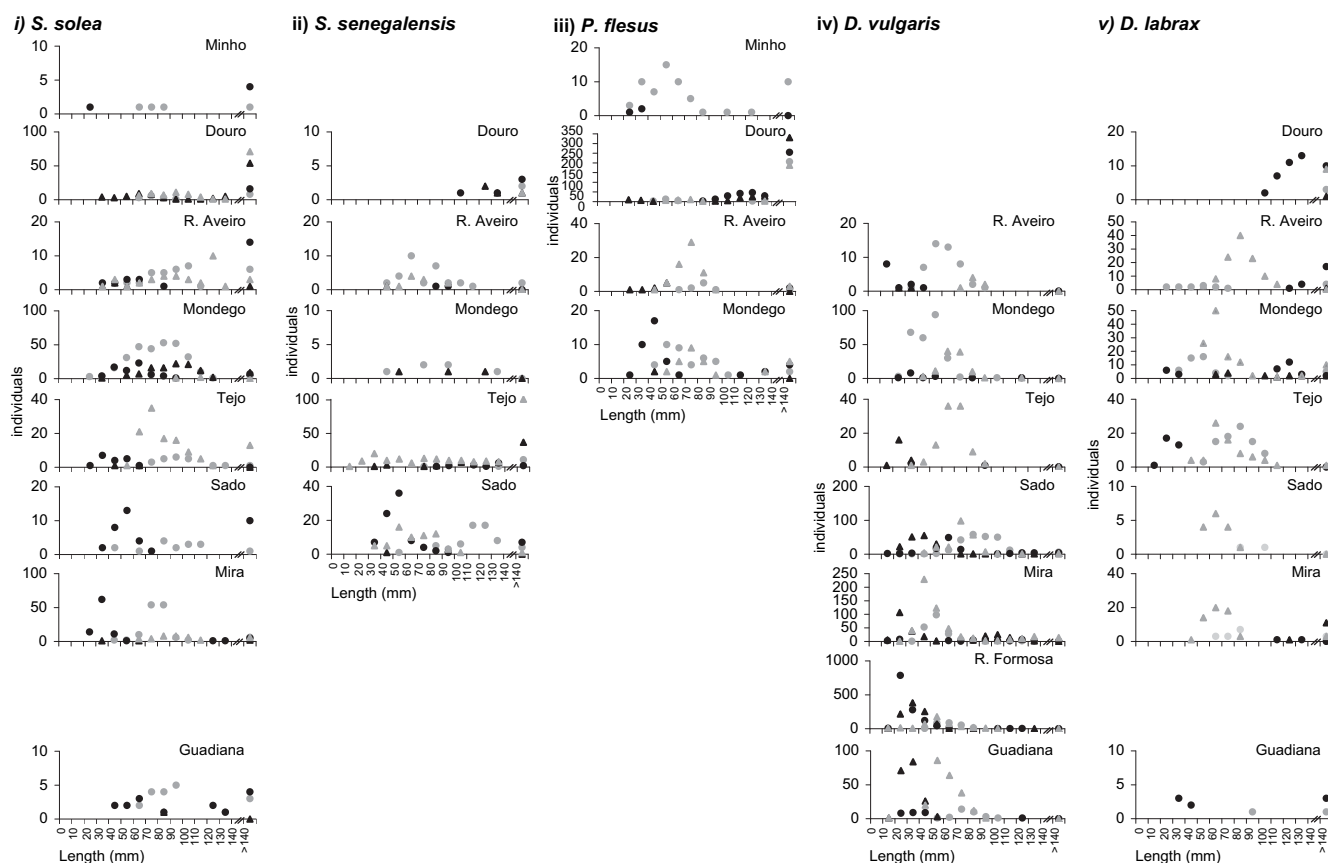
Environmental characteristics varied among and within estuaries. Despite notable variability among estuaries, estuarine gradients presented similar features and many sites had equivalent ranges of the measured parameters (Table 1).

Length frequency distributions of the five species were in most cases similar in all sampled sites within each estuary and plots were built disregarding site detail (Fig. 2). However, in some cases small intra-estuarine variation in length distribution was observed, namely for: *S. solea* in the Mondego estuary; *P. flesus* in the Minho;

*D. labrax* in the Tejo and *D. vulgaris* in the Mondego, Sado and Mira estuaries (results not shown). In most estuaries, the majority of caught individuals corresponded to 0-group lengths. Nevertheless, larger fish also occurred frequently in some of the estuaries, particularly: *S. solea* in the Douro, Ria de Aveiro and Tejo; *S. senegalensis* in the Tejo and Sado; and *P. flesus* and *D. labrax* in the Douro estuary. Increase in size of each species' 0-group was observed from May to July in both years, with length range differing with species. *Platichthys flesus* and *D. vulgaris* 0-group modal score lengths in May were slightly higher in southern than northern estuaries. Species' 0-group modal lengths in each month were mostly similar between sampling years (particularly evident in *D. vulgaris* and *P. flesus*).

The occurrence and density of each of the five selected species varied markedly amongst estuaries (Fig. 3). These estuaries were inhabited by several of these species, except the Minho and Ria Formosa where fewer occurred, with the dominance of at least one of them. Densities of the five species together were highest in the Ria Formosa (peak density was 539 individuals.1000 m<sup>-2</sup> in site c in July 2006) even if almost exclusively due to *D. vulgaris*, and in the Mondego and Mira estuaries. *Solea solea* and *Dicentrarchus labrax* occurred in most systems, *P. flesus* occurred in the four more





**Fig. 2.** Length frequency distributions (for 10 mm length interval classes) of i) *Solea solea*, ii) *Solea senegalensis*, iii) *Platichthys flesus*, iv) *Diplodus vulgaris* and v) *Dicentrarchus labrax* collected in May 2005 (▲), July 2005 (△), May 2006 (●) and July 2006 (◐) in estuarine systems along the Portuguese coast. Estuaries are presented from North to South.

northerly ones while *S. senegalensis* and *D. vulgaris* occurred mainly in central and southern estuaries, respectively. Overall, juvenile densities differed significantly among estuaries (except for *D. labrax*) (Table 2a). Although not significantly different, higher densities of *S. senegalensis* occurred in the Tejo and Sado, *D. vulgaris* in the Ria Formosa and *D. labrax* in the Mondego and Tejo. Significantly higher densities of *P. flesus* were found in the Douro and higher densities of *S. solea* occurred in the Douro, Mondego and Mira estuaries.

In most estuaries, species were present in specific sites (e.g. Ria de Aveiro, Mondego), whereas in others they occurred in most sites (e.g. Douro and Ria Formosa). Significant differences in densities amongst sites of an estuary were observed for all species in at least one of the estuaries (Table 2b).

Overall in a macro-scale spatial observation, regardless of the estuary: *S. solea* and *P. flesus* had higher densities in upper estuarine sites; contrarily *D. vulgaris* attained higher values in the lower estuary and some side channel sites. Although less evident, higher densities of *S. senegalensis* and *D. labrax* were found in upper estuary and side channel sites.

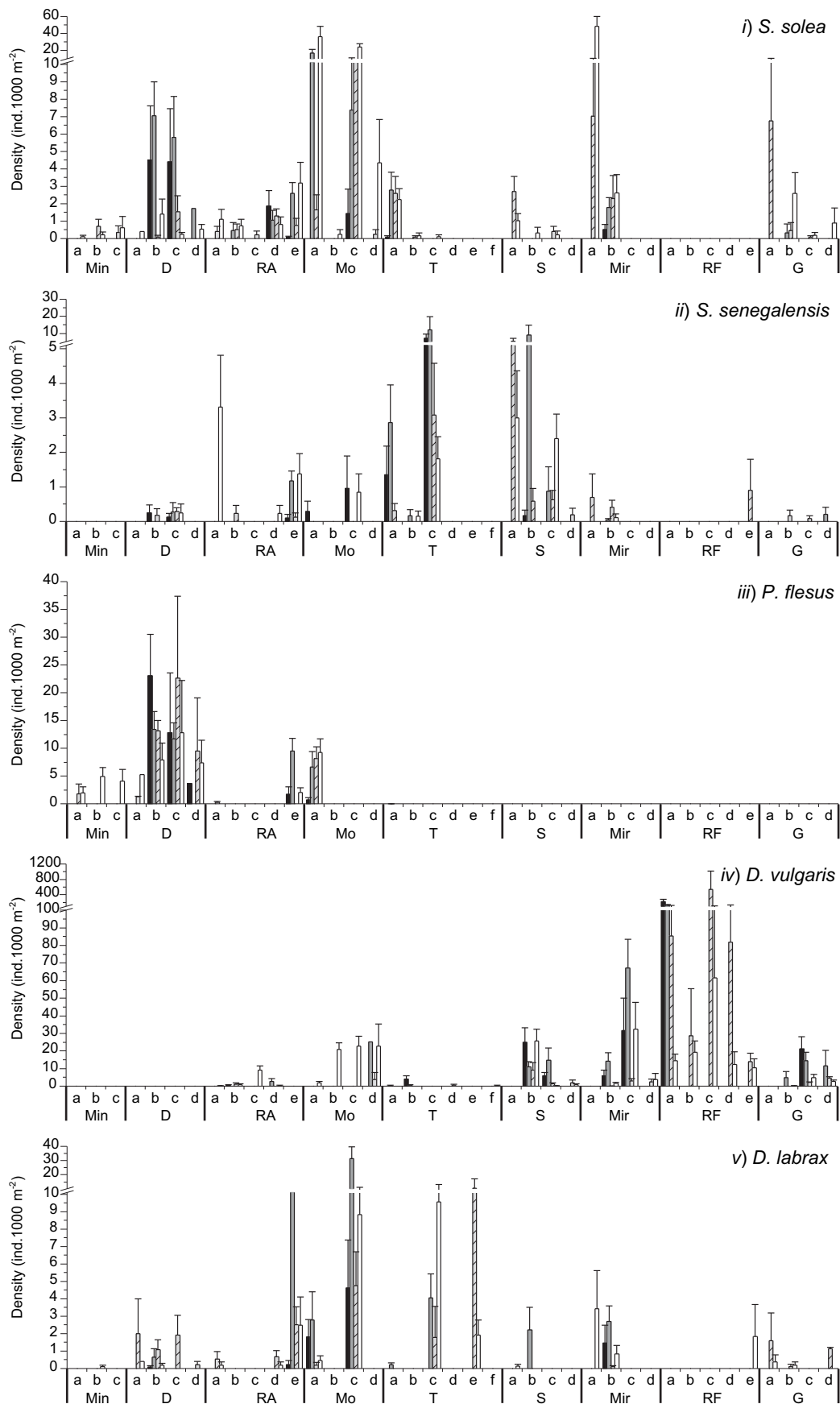
Despite the variations in density of each of the five species according to season and year, species distribution patterns within estuaries were maintained overall and enabled the identification of sites with consistently high densities throughout sampling periods (Table 3). This highlighted several important sites within each estuary and in many cases single species had more than one important site per estuary. In addition, identified important sites for juveniles were commonly used by multiple species simultaneously. The area occupied by high density sites differed greatly amongst estuaries. In general, large estuaries presented larger important sites for juveniles (e.g. Tejo 15.4 km<sup>2</sup> and Sado 8.4 km<sup>2</sup>) although overall

these corresponded to smaller proportions of the total estuarine area (4.8 and 4.7%, respectively). In contrast, estuaries with a channel like geomorphology had in general smaller important sites for juveniles (e.g. Douro 2.8 km<sup>2</sup> and Mira 1.4 km<sup>2</sup>) but these corresponded to larger percentages of the total estuarine area (28.0%).

The several fitted GLM varied markedly with species and also with estuary in the significance and percentage of deviance explained by the different predictors, both individually as well as in the best explanatory combination of predictors (Table 4). In general, species occurrence amongst sites within an estuary was significantly explained by environmental variables when species occurred in specific sites and overall environmental gradients were observed. This was the case in most estuaries; Minho, Douro and Ria Formosa were generally the exceptions. Moreover, the environmental variables associated with juvenile densities, considering only the sites where each analysed species occurred, differed greatly.

The occurrence of *S. solea* within an estuary was mostly explained by salinity or relative distance to the estuary mouth, along with some importance of depth, percentage of mud in the sediment, importance of intertidal areas and macrozoobenthos densities. Salinity and relative distance to the estuary mouth also explained some of the variability in occurrence amongst sites of all estuaries. Density variation within an estuary was explained by different predictors depending on the system, such as salinity, relative distance to the estuary mouth, depth or macrozoobenthos densities, whereas some of the variability amongst all estuaries was explained by salinity, importance of intertidal areas and macrozoobenthos densities.

The occurrence of *S. senegalensis* within estuaries where it was only found in specific sites (e.g. Ria de Aveiro and Tejo) was



**Fig. 3.** Mean (and standard error bars) density (individuals  $1000\text{ m}^{-2}$ ) of i) *Solea solea*, ii) *Solea senegalensis*, iii) *Platichthys flesus*, iv) *Diplodus vulgaris* and v) *Dicentrarchus labrax* in May 2005 (■), July 2005 (▒), May 2006 (▨) and July 2006 (□) in sites sampled within estuarine systems along the Portuguese coast: Min – Minho (a, b, c), D – Douro (a, b, c, d), RA – Ria de Aveiro (a, b, c, d, e), Mo – Mondego (a, b, c, d), T – Tejo (a, b, c, d, e, f), S – Sado (a, b, c, d), Mir – Mira (a, b, c, d), RF – Ria Formosa (a, b, c, d, e) and G – Guadiana (a, b, c, d).

**Table 2**

Significance tests for differences in densities of juvenile *S. solea*, *S. senegalensis*, *P. flesus*, *D. vulgaris* and *Dicentrarchus labrax* among and within estuaries: a) estuary as independent factor – Kruskal–Wallis non-parametric test for differences among groups and post-hoc comparison Dunn test for differences between pairs of groups (significantly different estuaries at  $P < 0.05$  are represented with different superscript numbers); b) site within each estuary as independent factor – Kruskal–Wallis non-parametric test for differences among groups. Estuaries are: Min – Minho, D – Douro, RA – Ria de Aveiro, T – Tejo, S – Sado, Mir – Mira, RF – Ria Formosa, G – Guadiana.

a) Factor: Estuary										
Species	Kruskal–Wallis test			Dunn test						
	P			Estuary						
<i>S. solea</i>	**			Min <sup>1</sup>	D <sup>1,2</sup>	RA <sup>1,2</sup>	Mo <sup>1,2</sup>	T <sup>1</sup>	S <sup>1</sup>	Mir <sup>1</sup> RF <sup>1,3</sup> G <sup>1</sup>
<i>S. senegalensis</i>	**			ns						
<i>P. flesus</i>	***			Min <sup>1</sup>	D <sup>2</sup>	RA <sup>1</sup>	Mo <sup>1</sup>	T <sup>1</sup>	S <sup>1</sup>	Mir <sup>1</sup> RF <sup>1</sup> G <sup>1</sup>
<i>D. labrax</i>	ns			na						
<i>D. vulgaris</i>	***			ns						
b) Factor: Site within an estuary										
Species	Estuary									
	Min	D	RA	Mo	T	S	Mir	RF	G	
<i>S. solea</i>	ns	ns	ns	ns	ns	ns	*	ns	ns	
<i>S. senegalensis</i>	ns	*	ns	ns	*	ns	ns	ns	ns	
<i>P. flesus</i>	ns	*	ns	**	ns	ns	ns	ns	ns	
<i>D. vulgaris</i>	ns	ns	ns	ns	ns	*	ns	ns	ns	
<i>D. labrax</i>	ns	ns	*	**	ns	ns	ns	ns	ns	

Significantly different estuaries at  $P < 0.05$  represented with different superscript numbers.

explained by different predictors, particularly depth, percentage of mud in the sediment, relative distance to the estuary mouth and macrozoobenthos density, whereas variability amongst sites of all estuaries was mostly explained by relative distance to the estuary mouth. Variability in density within an estuary was related to distinct predictors depending on the system, particularly depth, relative distance to the estuary mouth and macrozoobenthos density, whereas variability in density amongst all estuaries was related to depth and relative distance to the estuary mouth.

The presence of *P. flesus* within each estuary where it inhabited particular sites (e.g. Ria de Aveiro and Mondego) was mostly explained by salinity, depth and macrozoobenthos density, whereas occurrence amongst sites of all estuaries was mainly explained by salinity, depth, percentage of mud in the sediment, importance of intertidal areas, relative distance to the estuary's mouth and latitude. Variability in density within an estuary was related to predictors only in the Douro estuary, where it was associated with the percentage of mud in the sediment, relative distance to the estuary mouth and macrozoobenthos density, whilst variability amongst all estuaries was mostly related to depth, latitude and arthropoda density.

The occurrence of *D. vulgaris* within estuaries, with the exception of the Ria Formosa where it was quite evenly distributed, was largely explained by salinity and also by depth, percentage of mud in the sediment, importance of intertidal areas, relative distance to the estuary mouth and macrozoobenthos density, whereas variability amongst all estuaries was explained by salinity, presence of seagrass and latitude. Density within an estuary was related to several predictors namely salinity, depth, percentage of mud in the sediment, presence of seagrass, importance of intertidal areas and macrozoobenthos density, whilst variability amongst all estuaries was mainly related to percentage of mud in the sediment and presence of seagrass.

*Dicentrarchus labrax* was present in well defined sites in most estuaries and its occurrence within them was mostly explained by salinity, depth, percentage of mud in the sediment and macrozoobenthos density depending on the system; whereas variability amongst sites in all estuaries was largely explained by most of the

**Table 3**

Total estuarine area and area of the important sites for juvenile *Solea solea* (SS), *Solea senegalensis* (SN), *Platichthys flesus* (PF), *Diplodus vulgaris* (DV) and *Dicentrarchus labrax* (DL) identified in the analysed estuarine systems along the Portuguese coast (km<sup>2</sup> and percentage relative to total estuarine area).

Estuary	Total area (km <sup>2</sup> )	Important sites for juveniles					
		Area (km <sup>2</sup> )	SS (% of estuary area)	SN	PF	DV	DL
Minho	23	1.8	7.8	–	–	a, b, c	–
Douro	10	2.8	28.0	a, b	–	b, c	a, b, c
R. Aveiro	74	10.7	14.5	a, b, d, e	a, e	e	e
Mondego	10	0.9	9.0	a, c	c	a	b, c, d
Tejo	320	15.4	4.8	a	a, c	–	b
Sado	180	8.4	4.7	a	a, b, c	–	b, c
Mira	5	1.4	28.0	a, b	–	–	b, c
R. Formosa	91	3.5	3.8	–	–	–	a, b, c, d, e
Guadiana	20	4.2	21.0	a, b	–	–	c, d

predictors, in particular temperature, salinity, percentage of mud in the sediment and latitude. Variation in density within an estuary was also related to several abiotic and biotic predictors depending on the system, particularly depth, percentage of mud in the sediment and macrozoobenthos density. Amongst all estuaries this variability was related to most of the abiotic predictors, mainly depth and percentage of mud in the sediment.

#### 4. Discussion

Marine migrant species are an important component of fish diversity in estuaries along the Portuguese coast, as in most European estuarine fish assemblages (see review by Franco et al., 2008), and juvenile *S. solea*, *S. senegalensis*, *P. flesus*, *D. vulgaris* and *D. labrax* were consistently present in a large number of the analysed estuaries. These species' distributions depicted a differential use of the estuarine systems and areas within them, allowing the identification of important estuarine sites for juveniles of each species. Moreover, distributions also highlighted species-specific differences and identified species macro-scale estuarine use patterns and associated environmental variables. Key environmental features influencing juvenile distribution (occurrence and density) within estuaries were identified and varied depending on the system, although there were common dominant features for each species. Their variability among estuaries demonstrated species tolerance to different available environmental conditions. Inter-estuarine variability in each species occurrence and density was also in part explained by several environmental variables and these differed largely amongst species.

The slight decrease in 0-group modal lengths of *P. flesus* and *D. vulgaris* from southern to northern estuaries in May suggests a latitudinal trend in the date of estuarine colonization. A similar trend was demonstrated for *D. labrax* along this coast through otolith daily increments (Vinagre et al., 2009a), but this could not be confirmed in the present study. Such a trend in colonization is suggested to be related to a variation in sexual maturation and spawning season along the coast as a result of differences in water temperature and photoperiod (Vinagre et al., 2009a).

The occurrence of juveniles in an estuary is primarily a function of species distribution along the coast which defines the probability of larvae being transported from marine spawning grounds and colonizing an estuary. Adult distribution areas in the marine environment (Whitehead et al., 1989) were generally mirrored with the occurrence of juveniles in these estuaries along the Portuguese coast. Distribution areas of *S. solea* and *D. labrax* extend from Norway to Senegal and juveniles occurred in most estuaries; *P. flesus* distributes from Norway to Portugal and was found only in the four more northerly estuaries, whereas *S. senegalensis* and *D.*





Diplodus vulgaris																															
RA	92	–	–	ns	7	7	ns	–	ns	8	–	17	26	10	4	17	–	–	ns	ns	71	ns	–	–	ns	–	ns	ns	ns	19	
		dep + mud + int + dis	41	–	–	7	0	–	2	32	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
Mo	61	–	–	12	45	16	ns	–	ns	8	–	ns	8	12	ns	10	–	–	ns	ns	58	ns	–	–	58	52	–	ns	70	54	ns
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	58	–	–	–	–	–	–	–	12	–	
T	18	–	–	ns	ns	ns	ns	–	ns	ns	–	ns	ns	24	ns	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
S	97	–	–	ns	18	ns	13	–	23	16	–	6	21	ns	21	45	–	–	ns	ns	ns	20	–	ns	ns	–	21	23	ns	22	
		dis + mol	47	–	–	–	–	–	–	16	–	–	–	31	–	–	–	–	–	–	–	20	–	12	–	–	–	–	–	–	
Mir	74	–	–	ns	30	19	11	24	24	17	–	7	31	21	0	34	–	–	ns	37	18	25	22	22	ns	–	ns	25	25	ns	
		sal + ann	37	–	30	–	–	–	–	–	–	8	–	–	–	–	–	–	–	–	4	–	–	41	–	–	–	–	–	–	
RF	44	–	–	ns	ns	ns	ns	ns	ns	ns	–	–	–	–	–	123	–	–	–	36	13	ns	ns	18	–	ns	–	–	–	–	
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	13	–	–	24	–	–	–	–	–	–	
G	55	–	–	2	52	52	24	–	28	57	–	11	55	30	21	13	–	–	ns	ns	ns	ns	–	ns	ns	–	ns	ns	ns	ns	
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	14	34	–	–	–	–	–	–	–	
ALL	609	–	–	1	21	4	ns	11	3	9	13	–	–	–	–	456	–	–	–	10	16	ns	19	38	20	ns	15	–	–	–	
		sal + dep + sea + int+ lat	31	–	21	0	–	3	3	–	4	–	–	–	–	–	–	–	–	–	–	–	19	23	–	8	–	–	–	–	
Dicentrarchus labrax																															
Min	9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
D	32	–	–	ns	22	ns	ns	–	ns	ns	–	ns	ns	ns	ns	10	–	–	–	41	34	29	ns	–	–	ns	–	ns	ns	ns	
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	34	24	–	–	–	–	–	–	–	–	
RA	92	–	–	10	20	ns	ns	–	ns	ns	–	20	24	11	15	13	–	–	–	22	ns	31	29	–	ns	ns	–	23	23	28	27
		sal + ann	24	–	20	–	–	–	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
Mo	61	–	–	40	ns	22	49	–	ns	ns	–	50	8	ns	54	17	–	–	–	18	20	34	27	–	27	27	–	27	27	27	
		dep + art	31	–	–	22	–	–	–	–	–	–	10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
T	80	–	–	26	6	63	38	–	ns	ns	–	ns	ns	11	19	20	–	–	ns	ns	ns	ns	–	–	ns	–	–	–	–	–	
		sal + mud	58	–	6	–	52	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
S	18	–	–	ns	ns	ns	ns	–	ns	ns	–	ns	ns	ns	ns	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
Mir	43	–	–	22	ns	ns	8	ns	ns	12	–	ns	ns	ns	ns	7	–	–	–	63	ns	ns	54	–	–	54	–	54	54	54	
G	34	–	–	ns	10	ns	ns	–	ns	ns	–	27	0	27	27	3	–	–	–	ns	ns	ns	ns	–	–	–	ns	ns	ns	ns	
ALL	423	–	–	4	4	ns	4	ns	2	3	ns	3	0	2	1	101	–	–	–	3	5	12	25	–	9	ns	ns	ns	ns	ns	
		tem + sal + mud + int + lat + ann + art + ben	25	4	5	–	3	–	1	–	7	1	0	–	3	–	–	–	–	3	–	–	22	–	2	–	–	1	2	–	3

*vulgaris* distribute from the Bay of Biscay to Senegal and occurred mainly in the central and southern estuaries, respectively.

Overall, suitable estuarine grounds for juveniles are essential (Riou et al., 2001; Le Pape et al., 2003a). Salinity is a key environmental feature for species occurrence, as tolerance to it is limited physiologically, and determined species presence in the estuaries, as well as their major patterns of occurrence within each system. The rare occurrence of juvenile *D. vulgaris* in the Minho and Douro estuaries is likely to be due to extensive low salinity areas. However, the latter accounted for the dominance of *P. flesus* relatively to the remaining flatfish community in these two estuaries, as suggested for the Minho estuary by Freitas et al. (2009). Moreover, salinity gradients defined preferential estuarine areas for each species (as previously reported extensively for individual species, see e.g. Cabral and Costa, 2001; Horta et al., 2004; Vinagre et al., 2006; Freitas et al., 2009) and spatial segregation or overlap amongst species: *P. flesus* and *S. solea* in low to mesohaline areas and *D. vulgaris* in mesohaline to polyhaline areas. Distributions of *S. senegalensis* and *D. labrax* were less associated with salinity.

High prey availability is generally recognized as an important feature of habitat quality in juvenile grounds (Gibson, 1994). Concurrently, macrozoobenthos densities were, in several estuaries, associated with intra-estuarine variability in the occurrence and density of *S. solea*, *D. vulgaris* and *D. labrax*, as shown with the GLM approach. An increase in the explanatory ability of fish distribution models is often achieved by considering macrozoobenthos distribution maps in addition to abiotic features (Stoner et al., 2001; Le Pape et al., 2007), particularly on a small scale where many abiotic features are more homogeneous (Nicolas et al., 2007; Vinagre et al., 2009b), as in the present analysis. Furthermore, macrozoobenthos densities were associated with both the variability in fish densities within estuaries and amongst them, in the case of *S. solea* and *P. flesus*, and possibly influence the potential nursery function of each system.

Intertidal areas represent temporary feeding grounds for nekton during high tide and in some cases have higher macrozoobenthos densities than adjacent subtidal areas (França et al., 2008, 2009a). However, in the present study their size had in general a poor relationship with these fish species occurrence and density and a different sampling design will be required to evaluate their influence with further detail.

Sediment type can affect fish burial behaviour as well as prey and predator distributions and has been associated with species distribution as a result of habitat preferences and selection, particularly that of flatfish due to their close association with the bottom (Rogers, 1992; Neuman and Able, 1998; Stoner et al., 2001). Concurrently, in the present study the percentage of mud in the sediment was related to both intra- and inter-estuarine variation in most species' occurrence and density.

In addition to limiting the distribution of *P. flesus* to the northern estuaries, observed temperature gradients amongst and within estuaries along with species-specific optimum temperature range may have influenced fish distribution. Despite this, these relationships most probably resulted from co-occurring variability in other determinant environmental variables (Cabral and Costa, 1999, 2001). Similarly, depth related flatfish distributions have been described in estuaries and coastal areas (Stoner et al., 2001) as well as in the present study, though they are probably a result of co-occurring gradients of other factors rather than of a direct effect of depth.

Vegetated habitats, particularly seagrass beds, are acknowledged for high densities of juveniles of numerous fish species (see review by Minello et al., 2003) due to habitat preferences possibly related to lower predation pressure (Bell and Westoby, 1986). Concurrently, and since seagrass habitat was present only in lower estuary areas, *D. vulgaris* which is mostly found in lower estuary

sites presented markedly higher occurrence and density in estuaries and sites with seagrass.

Variability in categorical habitat types used by juveniles has been explored amongst estuaries (e.g. seagrass, saltmarsh, unvegetated sand/mud) (Goldberg et al., 2002; Minello et al., 2003; Lazzari, 2008; França et al., 2009b). However, few studies have addressed the variability of a species intra-estuarine use patterns as well as its relationship with continuous environmental variables amongst systems (Fodrie and Mendoza, 2006; Able and Grothues, 2007). Results evidence species' adaptability in occupying different site types. Overall, fish occupy the most suitable available habitat, i.e. realized niche (Hutchinson, 1959), that fulfils most of the species' preferences, i.e. fundamental niche (Hutchinson, 1957). However, the environmental features of these sites vary amongst estuaries. A striking result is that of *P. flesus*. It occurred in high densities in well defined segregated sites of an estuary (e.g. Ria de Aveiro and Mondego) as well as throughout all sites in other estuaries (e.g. Minho and Douro). In systems such as the latter, the GLM approach could only identify predictors with low percentages of explained variance.

Considering the observed variability, the individual analysis of multiple estuaries is therefore essential to identify environmental features decisive in structuring important sites for juveniles of each species and to evaluate consistency of intra-estuarine use. Spatial scale and sampling design is key to modelling species distributions as a response to environmental characteristics and results of this study highlighted that generalizing the importance of environmental characteristics in a given estuary to other systems or a different scale should be avoided. In addition, the present approach and data represent important background information for future research on spatially explicit models which should ultimately enable the prediction of species distribution responses to potential changes in environmental conditions and habitat disturbance or loss, both of natural or anthropogenic origin, as well as identifying essential areas for species conservation.

Estuarine sites used simultaneously by juveniles of several species were the most common and may be of increased value to management and conservation. Moreover, species segregation and overlap differ within and amongst estuaries as a result of their variability in estuarine use, and co-occurring species are likely to be affected by the same habitat alterations.

Recent reports of the mean and peak density of juveniles in putative nursery grounds in these and other estuaries along the European Atlantic coast (e.g. Cabral et al., 2007; Nicolas et al., 2007; Martinho et al., 2009) differ notably amongst estuaries and studies. Mean and peak densities are commonly between 10 and 100 individuals.1000 m<sup>-2</sup> and peak densities only seldom above 200 individuals.1000 m<sup>-2</sup>. Despite this wide disparity of values, present juvenile densities are within these ranges. Juveniles of these species (with the exception of *D. vulgaris*) have not been reported in exposed shallow zones along the Portuguese coast, even though elevated densities (10 individuals.1000 m<sup>-2</sup>) have been reported in other geographical areas (Le Pape et al., 2003a). Nevertheless, these are in general lower in comparison to those found in estuaries (Le Pape et al., 2003a). Caution is advised when comparing density amongst independent studies as these may be largely confounded, namely by sampling gear, time (day or night), and inter-annual variability in year-class strength and post-larvae settlement in nursery grounds.

High inter-annual variability in juvenile densities and year-class strength has been frequently reported (van der Veer et al., 2000) and also found in these systems and species (Costa and Cabral, 1999; Cabral et al., 2007; Dolbeth et al., 2008). It has been associated with the variation in transport and survival of eggs and larvae, influenced both by wind and hydrodynamic circulation, and settlement success in potential nursery grounds (Nielsen et al.,

1998; Martinho et al., 2009). Annual rainfall influences river flow and, consequently, estuarine salinity conditions, and has also been reported to greatly affect suitable habitat availability and the number of juveniles in coastal (Le Pape et al., 2003b) and estuarine grounds (Vinagre et al., 2007; Dolbeth et al., 2008; Martinho et al., 2009). Despite the inter-annual variability in density observed in some of the estuarine sites, the relative importance of the analysed estuaries, or of sites within each estuary, was in general maintained. This variation is possibly related to changes in environmental conditions, in particular rainfall, as 2005 was classified as an extremely dry year and 2006 normal (Instituto de Meteorologia, 2006, 2007). In the end, a wider set of sampling years will be required to explore the importance of specific features regarding inter-annual variation.

Analysing fish species at their latitudinal limits of distribution raises particular interest as population tendencies may be revealed at small spatial and temporal scales (Dorel and Désaunay, 1991). *Platichthys flesus* is currently rare south of the Mondego estuary whereas only two decades ago it was abundant in the Tejo (Costa and Bruxelas, 1989; Cabral et al., 2001). Its occurrence in a smaller number of estuaries is likely a disadvantage for the stability of adult flounder coastal stocks along the Portuguese coast, particularly in the case of changes in these systems.

In addition to its influence on the use of estuarine areas by juveniles, habitat quality is reported to have a combined influence with habitat quantity (Gibson, 1994). Habitat quantity is a key feature of nursery grounds, with recruitment levels related to their area, particularly in flatfish (Rijnsdorp et al., 1992; Gibson, 1994). Presently analysed estuaries differed largely in total area, area of important sites for juveniles of a species as well as in the percentage of the estuarine area these sites represent, which also varied amongst species. Consequently, since higher densities of juveniles often occur in sites with smaller areas, which is then reflected in the total number of juveniles in that site, evaluating suitable habitat quantity variations amongst estuaries may alter the perspective of their potential importance as measured only by juvenile densities.

The identification of important estuaries and sites for juveniles is essential to the design of efficient management and conservation plans and should be defined considering the intended protection objectives, namely if these are directed to the meta-population of a particular species, several species or to estuarine nursery function as a whole. However, the density of juveniles in estuaries alone does not provide information on enhanced juvenile growth or on the number of individuals effectively recruiting to adult subpopulations; even if it is generally used to measure production of juvenile sites, i.e. putative nurseries, estimate the potential number of juveniles leaving an estuary to adult coastal stocks (Dolbeth et al., 2008) and compare the contribution of different estuaries to adults stocks (Riou et al., 2001; Le Pape et al., 2003a; Rooper et al., 2004). As defined by Beck et al. (2001), in order to adequately assess if these estuaries and identified important sites for juveniles are in fact nursery areas, it is necessary to determine their effective contribution to coastal adult stocks. Otolith elemental signatures, which have been successfully used as natural tags of habitat use enabling the retrospective identification of estuarine nursery source (see review by Elsdon et al., 2008), have provided firsthand evidence regarding the differential contribution of these estuaries to marine adult subpopulations of these species (Vasconcelos et al., 2008).

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