Cah. Biol. Mar. (2004) 45 : 213-224

Comparison of the fish assemblages in tidal salt marsh creeks and in adjoining mudflat areas in the Tejo estuary (Portugal)

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Abstract: A comparative analysis of the fish assemblages in two tidal salt marsh creeks and in the adjoining mudflat areas was conducted, based on two years of sampling surveys performed in different years, using a fyke net and a beam trawl, respectively. Fish species richness was higher in the mudflat areas (27 species) than in the tidal creeks (14 species). *Liza ramada* and *Pomatoschistus microps* were the most abundant species in tidal creeks, while the adjoining tidal flats were dominated by *P. microps* and *Pomatoschistus minutus.* The seasonal pattern of variation was different in the two habitat types. The main differences observed were mainly related with peak abundance of resident species and periods of estuarine colonization by juveniles of marine species that used the estuary as nursery area. The results obtained emphasize the importance of intertidal creek habitat within the estuarine environment for some fish species, particularly as juveniles. The utilization of this habitat is mainly related with feeding and predation avoidance.

Résumé: *Comparaison des assemblages ichtyques entre les chenaux de marée des marais salés et les vasières contigües dans l'estuaire du Tage (Portugal).* Une analyse comparative des communautés de poissons dans deux chenaux de marée de marais salés sous l'influence de la marée, ainsi que dans leurs secteurs contigus de bancs de vase, a été réalisée à partir de deux ans d'échantillonnages effectués au cours d'années différentes en utilisant, respectivement, un verveux et un chalut à perche. La richesse spécifique des poissons est plus élevée sur les vasières (27 espèces) que dans les chenaux de marée (14 espèces). *Liza ramada* et *Pomatoschistus microps* sont plus abondantes dans les chenaux de marée, alors que *P. microps* et *Pomatoschistus minutus* le sont dans les secteurs contigus. Le modèle de variation saisonnière est différent entre les deux types d'habitat. Les principales différences sont observées lors de l'abondance maximale des espèces résidentes et pendant les périodes de colonisation de l'estuaire par les juvéniles des espèces marines qui l'utilisent comme nourricerie. Les résultats obtenus soulignent l'importance des chenaux de marée de marais dans l'estuaire pour certaines espèces de poissons, en particulier pour leurs juvéniles. Cet habitat est essentiellement utilisé par ces espèces en relation avec l'alimentation, ainsi que l'évitement de la prédation.

Keywords: Fish assemblages, Tidal creeks, Mudflats, Tejo estuary, Portugal

Reçu le 17 juin 2003 ; accepté après révision le 21 avril 2004
Received 17 June 2003; accepted in revised form 21 April 2004.

Introduction

The importance of salt marshes as nursery habitats for fish has been emphasized by several authors, mainly for eastern USA estuarine systems (e.g., Cain & Dean 1976; Weinstein & Brooks 1985; Rozas 1995).

For European estuaries, some studies concerning the structure and dynamics of the fish assemblages in salt marsh areas were also developed, namely those conducted by Labourg et al. (1985), Drake & Arias (1991), Cattrijsse et al. (1994) and Costa et al. (1994). Despite these contributions, our knowledge of the fish assemblages in European salt marsh habitats is poor.

Salt marsh tidal creeks are unstable environments due to fluctuations of water level and current direction and velocity, which result in highly variable conditions (Labourg et al., 1985). Thus, the use of tidal creeks by fishes is controlled by the hydroperiod. During high tide, the creeks are flooded, allowing the access of fishes. At low tide, the water drains almost completely and fishes are forced to move to the adjoining subtidal areas.

The utilization of these habitat types may be discussed in terms of cost-benefit. The high instability of abiotic factors and the risk of stranding are selective factors for the occurrence of several species of fish. Species that tolerate such conditions can benefit of the high food availability induced by the extreme productivity of these marsh areas (Shenker & Dean, 1979). This fact associated with the low predation pressure within those habitats emphasizes their potential as feeding grounds and refuges for fish (Cain & Dean, 1976; Shenker & Dean, 1979; Bozeman & Dean, 1980).

The fish assemblages in salt marsh areas change seasonally as pulses of transient estuarine species colonize these shallow and intertidal areas (Bozeman & Dean, 1980; Rozas, 1995).

The role of the Tejo estuary as nursery for fish, particularly the upper areas, has been reported in a large number of studies (e.g., Costa, 1982; Costa & Bruxelas, 1989; Cabral, 1998; Costa & Cabral, 1999). According to these studies, the most important nursery grounds, where juveniles occur with high densities, are located in the adjoining areas of salt marshes. The most abundant fish species that use these nursery grounds are sea bass, *Dicentrarchus labrax* (Linnaeus, 1758), and soles, *Solea solea* (Linnaeus, 1758) and *Solea senegalensis* Kaup 1858. However, no studies focused on the role of the salt marsh areas for fish assemblages.

Here, we present a comparative analysis of the fish assemblages in two salt marsh tidal creeks and their adjoining mudflat areas in order to understand the importance of these habitat types for the fish community of the Tejo estuary.

Material and methods

Study Area

The Tejo estuary has an area of 320 km², of which 113,8 km² are intertidal. About 13 km² of the intertidal area is covered by salt marsh vegetation (Catarino et al., 1985). The Tejo estuary is mesotidal with semi-diurnal tides and a tidal range of about 4 m.

The present study was carried out in two salt marsh areas located in the upper part of the estuary (Fig. 1). This region is characterized by an extensive area of mudflats composed of fine muddy sediments, with 90,6% of particles with less than 20 µm diameter (Brotas et al., 1995). On the upper part of the mudflats, the pioneer/lower marsh areas are dominated by *Spartina maritima* Linnaeus while the middle marsh is mainly composed by *Halimione portulacoides* Linnaeus and *Arthrocnemon perenne* Miller, especially along the creeks.

Samples were taken in two tidal creeks (Hortas & Ponta da Erva) and the adjacent mudflat areas (Fig. 1). The creeks beds are approximately 150 m long, 15 m wide at the mouth and the height between the mud bottom and the marsh surface is ca. 1.5 m.

Both creeks have no connection with other neighbouring creeks, dewatering almost completely during ebb tides.

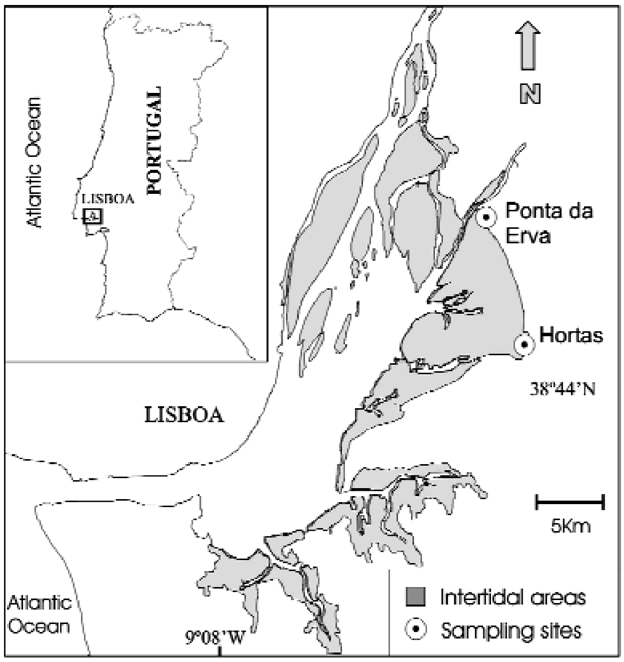

Figure 1. Location of the Tejo estuary and sampling sites.

Figure 1. Localisation des stations d'échantillonnage dans l'estuaire du Tejo.

Sampling methods

Two different sampling methods were used due to the particular characteristics of each of the habitats, i.e. salt marsh creeks and mudflats. In the creeks, samples were taken monthly, from September 1998 until August 1999, and quarterly from September 1999 until August 2000, during daylight at ebb tides of similar amplitudes, using fyke and gill nets (3 mm and 50 mm mesh size, respectively). The gill nets, that were seted in front of the fyke net opening, were used to capture the large specimens, mainly mugilids, to avoid clogging of the fyke net which completely blocked the creek mouths. Fishes were collected at 30 min intervals, from high tide until the creek was completely dewatered. At each collection, temperature and salinity were measured using a Hydrolab™ multiprobe sonde.

In the mudflat areas, samples were taken monthly from January 1995 until December 1996 at ebb tides using a 4 m beam trawl with 10 mm mesh size (stretched mesh) and one thicker chain. Trawls were towed at a speed of 1 knot and had 20 min duration. Temperature and salinity were also measured at each sampling period and area. All fishes caught were counted, measured (total length to the nearest 1 mm) and weighed (wet weight 1 mg precision) at the laboratory.

Data analysis

The nature of the abundance estimates obtained for salt marsh creeks and mudflat areas differed due to the particularities of each sampling technique. Salt marsh creeks data represent average values of catches performed during a complete ebb tide sampling, while data obtained for mudflats represent average values of beam-trawl catches per month. Due to these differences, comparisons between the two habitats were based on relative abundance values.

In order to analyse temporal changes in fish assemblages, months were grouped into seasons (autumn: September-November; winter: December-February; spring: March-May; summer: June-August).

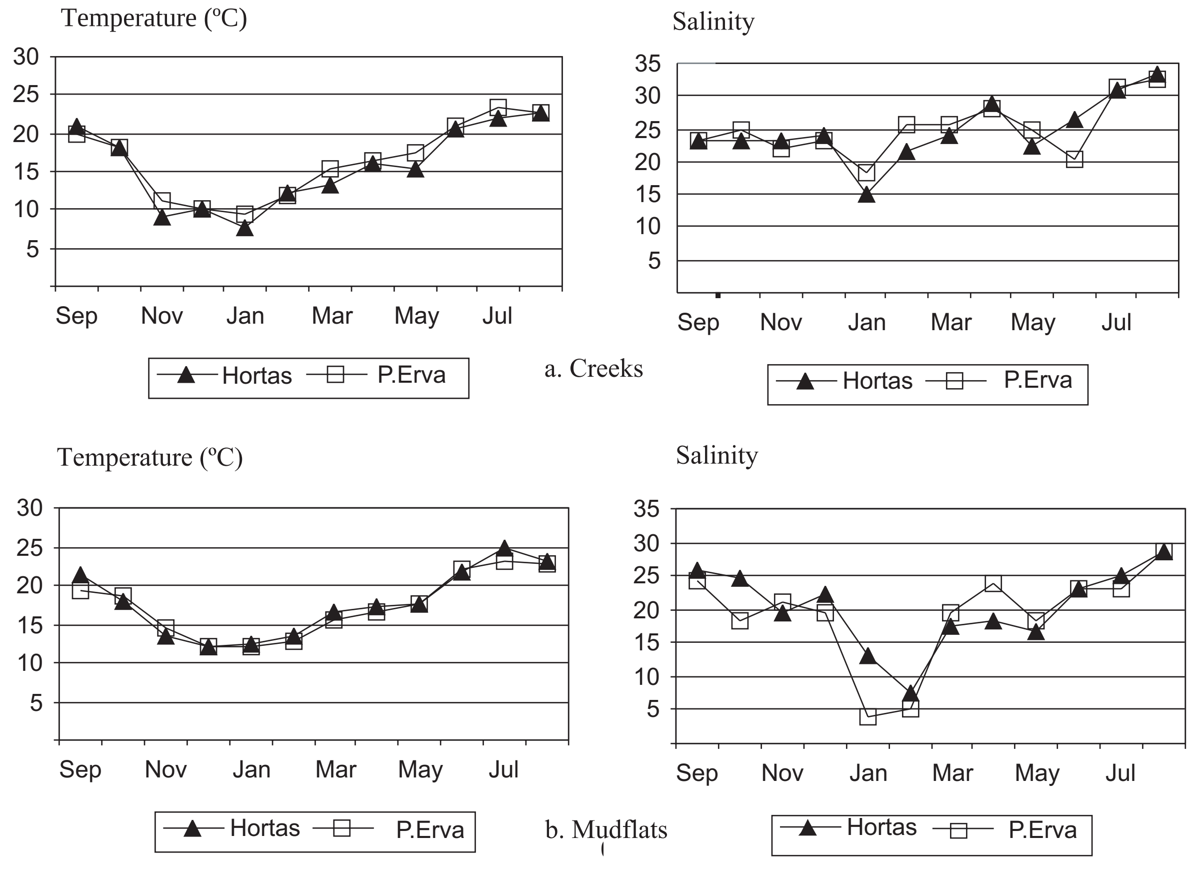

Figure 2. Water temperature and salinity in the study sites during the sampling period.
Figure 2. Température et salinité de l’eau aux sites échantillonnés durant la période de l’étude.

Spearman rank correlation coefficient (Zar, 1984) was calculated to compare the species ranking according to abundance in the creeks and in the mudflats.

The analysis of the structure of the fish assemblages was based on ecological (adapted from Potter et al., 1986) and trophic guilds, indicating the species' use of the estuary and their main feeding habits, respectively. Five ecological guilds (i.e. FW - fresh water; C – catadromous; E – estuarine resident; O - marine estuarine-opportunistic; M – marine straggler) and four trophic guilds (i. e. D - detritivorous; P - planktivorous; M – benthic macroinvertebrate feeders; FD - fish and decapods feeders) were used.

Species richness (S) (total number of species), Pielou's evenness (J) and Shannon-Wiener's (H') (using $\log_2$) diversity indices were calculated for each site and season (Ludwig & Reynolds, 1988).

The spatial and temporal variation in fish assemblage was evaluated using a correspondence analysis (CA) (Ter Braak & Prentice, 1988). Since results of the CA are affected by the presence of rare species (Ter Braak & Verdonschot, 1995), the values relative to those species were downweighed.

Table 1. Relative abundance and biomass (in percentages), ecological guilds (EG) (i.e. FW - freshwater; C – catadromous; E – estuarine; O - marine estuarine-opportunistic; M – marine straggler) and trophic guilds (TG) (i. e. D - detritivorous; P - planktivorous; M – macro invertebrate feeder; FD – fish and decapods feeders) of the fish species captured in the salt marsh creeks and in the mudflat areas at Hortas and Ponta da Erva. Ind – number of individuals.

Tableau 1. Abondance et biomasse relatives, guildes écologiques (EG) (Fw – eau douce; C – catadromes; E – résidant estuaire; O - marins estuariens-opportunistes; M – marins) et guildes trophiques (TG) (D - détritivores; P - planctivores; M – s'alimentant de macro-invertébrés; FD – piscivores et s'alimentant de décapodes) des espèces de poissons capturés dans les chenaux de marée et les vasières de Hortas et Ponta da Erva. Ind - Nombre d'individus.

			Hortas				Ponta da Erva			
			Creek		Mudflat		Creek		Mudflat	
Species	EG	TG	Ind.	Biomass	Ind.	Biomass	Ind.	Biomass	Ind.	Biomass
Anguilla anguilla	C	FD	0.2	< 0.1	0.1	1.5	< 0.1	0.1	0.4	2.3
Atherina presbyter	E	P	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	0.1	< 0.1	< 0.1
Barbus bocagei	FW	M							< 0.1	1.1
Chelon labrosus	O	D			< 0.1	0.7			0.1	3.6
Ciliata mustela	O	FD			< 0.1	0.1			< 0.1	0.1
Conger conger	O	FD			< 0.1	0.1			< 0.1	0.1
Dicentrarchus labrax	O	M	0.2	< 0.1	7.7	4.8	< 0.1	< 0.1	1.0	0.9
Diplodus bellottii	O	M							0.1	< 0.1
Diplodus sargus	O	M	< 0.1	< 0.1					0.1	0.2
Diplodus vulgaris	O	M							< 0.1	< 0.1
Engraulis encrasicolus	E	P	0.1	< 0.1	0.8	0.6	0.2	< 0.1	2.0	0.8
Gambusia holbrooki	FW	P	< 0.1	< 0.1			< 0.1	< 0.1		
Gobius niger	E	M			0.1	0.1			0.6	0.3
Halobatrachus didactylus	E	FD							< 0.1	< 0.1
Hippocampus hippocampus	E	P			< 0.1	< 0.1			< 0.1	< 0.1
Liza aurata	O	D	0.1	< 0.1	0.1	0.3	< 0.1	2.4	0.1	0.2
Liza ramada	C	D	35.2	99.5	6.0	55.3	1.7	89.0	4.9	56.6
Mugil cephalus	O	D	< 0.1	0.2	0.1	0.7			0.4	12.9
Platichthys flesus	O	M			0.3	2.2			0.1	0.5
Pomatoschistus minutus	E	M	< 0.1	< 0.1	9.8	1.1	< 0.1	< 0.1	24.1	2.6
Pomatoschistus microps	E	M	63.3	0.3	58.7	3.0	89.6	6.6	57.6	2.2
Raja clavata	M	FD			< 0.1	< 0.1			< 0.1	0.5
Sardina pilchardus	O	P	0.6	< 0.1	< 0.1	< 0.1	8.4	1.8	0.1	< 0.1
Solea senegalensis	O	M	< 0.1	< 0.1	15.0	29.0			5.5	13.4
Solea solea	O	M			0.1	0.2			0.5	1.2
Sparus aurata	O	M			0.1	0.1			< 0.1	0.2
Syngnathus typhle	E	P			< 0.1	< 0.1				
Syngnathus sp.	E	P	0.4	< 0.1	1.0	0.1	0.1	< 0.1	2.2	0.1
Total (number, weight in kg)			73905	1649	13572	143	241841	104	7079	96

For the most abundant species, the percentage of juvenile and adult individuals was determined based on length at maturity reported by Almeida (1996) for *Liza ramada* (Risso, 1826), Pestana (1989) for *Sardina pilchardus* (Walbaum, 1792), Dinis (1986) for *S. senegalensis*, and Bouchereau *et al.* (1990, 1993) for *Pomatoschistus minutus* (Pallas, 1770) and *Pomatoschistus microps* (Krøyer, 1838).

Results

Abiotic conditions

The variation of the temperature values was similar in the two creeks as well as in the two mudflat areas (Fig. 2). In both habitats, the maximum values were obtained in July and August (23.3ºC and 22.5ºC in Hortas and Ponta da Erva creeks, and 23.2ºC and 24.8ºC in the respective mudflat areas). The minimum values were recorded from November to February and were lower in the creeks (7.8ºC and 9.5ºC) compared to both mudflat areas (12.0ºC).

The maximum and minimum salinity values were obtained in the same months as the extreme temperature values. The distinct extremes in the salinity values were associated with the distinct periods of sampling, in the creeks the sampling procedures started in the beginning of the ebb tide whereas in the mudflats sampling was initiated with 2 hours of ebbing. Nevertheless the seasonal pattern of variation was similar in both areas (Fig. 2).

Tidal creeks: community structure

A total of 14 species occurred in the salt marsh creeks (Table 1), 14 in Hortas and 11 in Ponta da Erva. Species composition in the two intertidal creeks was similar and their species rank of abundance was correlated ($r = 0.937$; $p < 0.05$). *Mugil cephalus* Linnaeus 1758, S. *senegalensis* and *Diplodus sargus* (Linnaeus, 1758) only occurred at Hortas creeks**.** The fish assemblage in the tidal creeks was mainly composed by estuarine resident species and marine estuarine-opportunistic species that used the estuary as nursery area (Fig. 3). Freshwater species occurred only in periods of intense rainfall, while marine stragglers were absent from these areas.

Benthic macroinvertebrate feeders and planktivorous species were the predominant trophic groups in the creeks (Fig. 4). This last group was especially well represented at Ponta da Erva (about 50% of the number of species). *Anguilla anguilla* (Linnaeus, 1758) was the only species within the fish and decapods feeder category. Mugilidae were the only detritivores found in the creeks.

Two species were numerically dominant in the creeks (Table 1), comprising over 90% of the total number of individuals captured: *P. microps*, in both creeks (63.3% and

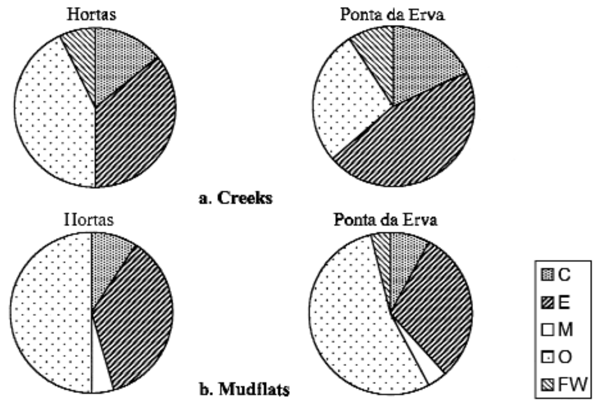

Figure 3. Distribution of the fish species per ecological guilds (Fw - fresh water; C – catadromous; E – estuarine resident; O - marine estuarine-opportunistic; M – marine straggler) for the salt marsh creeks and for the mudflats at Hortas and Ponta da Erva.

Figure 3. Distribution des espèces de poissons par guildes écologiques (Fw – eau douce; C – catadromes; E – résidents estuaire; O - marins estuaire-opportunistes; M – marins occasionnels) dans les chenaux de marée et les vasières de Hortas et Ponta da Erva.

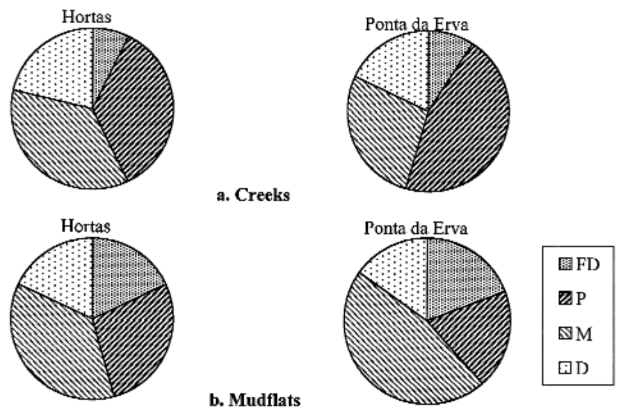

Figure 4. Distribution of the fish species per trophic guilds (D - detritivorous; P - planktivorous; M – macro invertebrate feeders; FD - fish and decapods feeders) for the salt marsh creeks and for the mudflats at Hortas and Ponta da Erva.

Figure 4. Distribution des espèces de poissons par guildes trophiques (D - détritivores; P - planctivores; M – s'alimentant de macro-invertébrés; FD – piscivores et s'alimentant de décapodes) dans les chenaux de marée et les vasières de Hortas et Ponta da Erva.

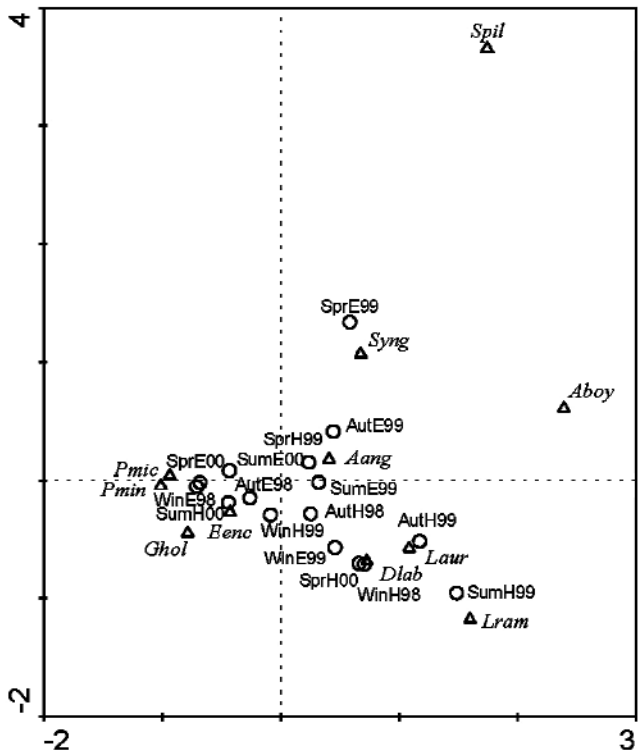

Figure 5. Ordination diagram of the first two canonical axes of the correspondence analysis performed on species abundance data (Aut – Autumn; Win – Winter; Spr – Spring; Sum – Summer; H – Hortas area; E – P. da Erva area; 98, 99 and 00 - sampling year; Aang – *A. anguilla*; Aboy – *A. boyeri*; Dlab – *D. labrax*; Eenc – *E. encrasicholus*; Ghol – *G. holbrooki*; Laur – *L. aurata*; Lram – *L. ramada*; Pmic – *P. microps*; Pmin – *P. minutus*; Spil – *S. pilchardus*; Sysp - *Syngnathus* sp). Horizontally – first ordination axis, Vertically – second ordination axis.

Figure 5 Diagramme de Classification des deux premiers axes canoniques de l'analyse de correspondance exécutée sur l'abondance d'espèces (Aut – Automne; Win – Hiver; Spr – Ressort; Sum – Eté; H – Hortas; E – P. da Erva; 98, 99 et 00 – année d'échantillonnage; Aang – *A. anguilla*; Aboy – *A. boyeri*; Dlab – *D. labrax*; Eenc – *E. encrasicholus*; Ghol – *G. holbrooki*; Laur – *L. aurata*; Lram – *L. ramada*; Pmic – *P. microps*; Pmin – *P. minutus*; Spil – *S. pilchardus*; Sysp - *Syngnathus* sp). Horizontalement - premier axe d'ordination, verticalement - deuxième axe d'ordination.

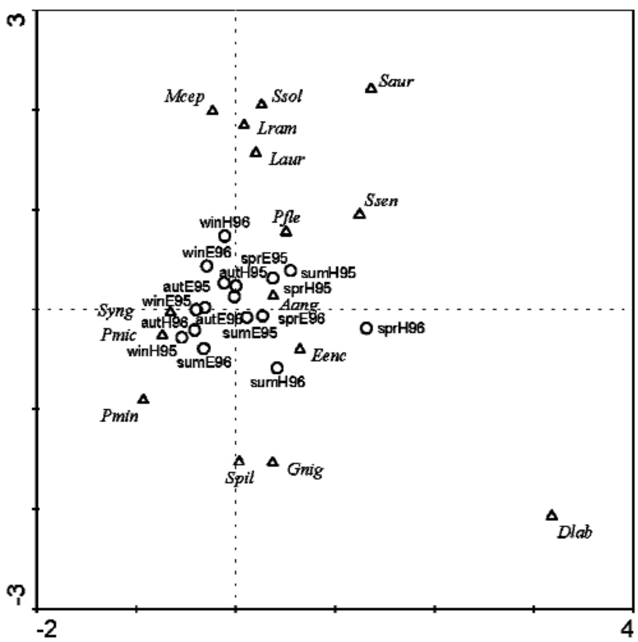

Figure 6. Ordination diagram of the first two canonical axes of the correspondence analysis performed on species abundance data (Aut – Autumn; Win – Winter; Spr – Spring; Sum – Summer; H – Hortas area; E – P. da Erva area; 95 and 96 - sampling year; Aang – *A. anguilla*; Aboy – *A. boyeri*; Dlab – *D. labrax*; Eenc – *E. encrasicholus*; Gnig – *G. niger*; Laur – *L. aurata*; Lram – L. *ramada;* Mcep – *M. cephalus*; Pfle – *P. flesus*; Pmic – *P. microps*; Pmin – *P. minutus*; Saur – *S. aurata*; Spil – *S. pilchardus*; Ssen – *S. senegalensis*; Ssol – *S. solea*; Sysp - *Syngnathus* sp). Horizontally – first ordination axis, Vertically – second ordination axis.

Figure 6. Diagramme de Classification des deux premiers axes canoniques de l'analyse de correspondance exécutée sur l'abondance d'espèces (Aut – Automne; Win – Hiver; Spr – Ressort; Sum – Eté; H – Hortas; E – P. da Erva; 95 et 96 – année d'échantillonnage; Aang – *A. anguilla*; Aboy – *A. boyeri*; Dlab – *D. labrax*; Eenc – *E. encrasicholus*; Gnig – G. niger; Laur – *L. aurata*; Lram – *L. ramada*; Mcep – *M. cephalus*; Pfle – *P. flesus;* Pmic – P. microps; Pmin – *P. minutus*; Saur – *S. aurata*; Spil – *S. pilchardus*; Ssen – *S. senegalensis*; Ssol – *S. solea*; Sysp - *Syngnathus* sp). Horizontalement - premier axe d'ordination, verticalement - deuxième axe d'ordination.

89.6% respectively for Hortas and Ponta da Erva), and *L. ramada*, mainly in Hortas (35.2%).

Considering biomass, *L. ramada* was the most important species representing 89% and 99.5% of the total, respectively for Hortas and Ponta da Erva creeks. *Liza aurata*, *P. microps* and *S. pilchardus* presented also high values compared to the other species, but considerably lower in relation to the value of *L. ramada*. The total biomass registered for Hortas was more than 15 times higher compared to the value obtained for Ponta da Erva.

Tidal creeks: seasonal variation

The seasonal variation pattern of the diversity index (H') was different in each creek (Table 2). For Hortas, higher values occurred during the autumn, when species richness and eveness were high. In summer, diversity was low due

Table 2. Mean seasonal values of specific richness (n), Shannon-Weaver`s index (H') and evenness (J) for the mudflat areas at Hortas and Ponta da Erva.

Tableau 2. Valeurs moyennes saisonnières de la richesse spécifique (n), de l'indice de Shannon-Weaver (H') et de l'indice d'équitabilité (J) des chenaux de marée et des vasières de Hortas et Ponta da Erva.

		Creek			Mudflat		
	Season	n	H'	J	n	H'	J
Hortas	Autumn	11	0.34	0.32	19	0.43	0.35
	Winter	5	0.34	0.48	13	0.44	0.39
	Spring	8	0.38	0.42	14	0.64	0.55
	Summer	9	0.25	0.26	16	0.69	0.57
P. Erva	Autumn	10	0.46	0.46	20	0.51	0.39
	Winter	6	0.12	0.16	12	0.47	0.44
	Spring	9	0.17	0.18	19	0.76	0.60
	Summer	7	0.23	0.27	20	0.55	0.42

to a decrease in evensess values. For Ponta da Erva, the lowest diversity values were observed during winter, when evenness was extremely low, and the highest values were obtained in spring and summer.

The ordination diagram that resulted from the CA (Fig. 5) reflected a weak seasonal pattern: the points relative to spring and summer periods were located mainly on the edges of the diagram. Nevertheless, points relative to spring and summer periods of 1999 sampling year were mainly located in the right side of the axis origin, associated with species such as *S. pilchardus*, *Syngnathus* sp. and *A. boyeri*.

The majority of the species presented their highest abundance values in spring and summer and only occurred in the creeks during part of the year, mainly as juveniles (Table 3).

The highest abundance of *P. microps* in the creeks was observed during spring, mainly in Ponta da Erva, with a population composed mostly of juveniles. In the late summer, there was a decrease in the abundance of this species and adults in the areas were scarce. During the end of autumn and winter a slight increased in the number of individuals was observed, mainly due to an influx of adults.

L. ramada was always present in the creeks with high numbers of individuals. Nevertheless, the abundances in Hortas were always higher than in Ponta da Erva. The exception was during spring when similar abundances, mostly small juveniles, were observed for both creeks. In the summer in Hortas, there was an increase in the number of both juveniles and adults captured. In the autumn and winter, there was a gradual decrease in the abundance and mostly adults were present in these areas.

S. pilchardus was present, mostly in Ponta da Erva, from the beginning of the spring until early autumn. The highest abundance of this species was observed during the spring when small juveniles began to appear in the area. In the summer, a marked decrease in the number of individuals was observed leading almost to the disappearance of the species from these areas.

Mudflats: community structure

Twenty seven fish species were identified in the mudflat areas (Table 1), 22 in Hortas and 26 in Ponta da Erva. Five species only occurred at Ponta da Erva: *Barbus bocagei* Steindachner 1864, *Diplodus bellottii* (Steindachner, 1882), *D. sargus*, *D. vulgaris* and *Halobatrachus didactylus* (Bloch & Schneider, 1801); and *Syngnathus typhle* was not found in this area. Nevertheless, there was a correlation in the species rank of abundance between the two mudflats ($r = 0.345$; $p < 0.05$). Marine estuarine-opportunistic species represented more than 50% of the fish species found in the mudflat areas (Fig. 3) and the contribution of estuarine residents was ca. 30%.

Raja clavata was the only marine straggler species represented in the sampled areas. *Gambusia holbrooki* was the only species found in the creeks that was absent from the mudflat areas.

Considering trophic guilds (Fig. 4), the benthic macroinvertebrate feeders were the predominant group, representing 37% of the total number of species in Hortas and 47% in Ponta da Erva. The other trophic groups presented a relatively equable importance.

P. microps was also the most abundant species in both mudflat areas, representing more than 50% of the catches (Table 1). *P. minutus* was more abundant in Ponta da Erva (24.1%), whereas *L.* ramada, *D. labrax* and *S. senegalensis* (6.0%, 7.7 % and 15.0%, respectively) were particularly abundant in Hortas.

In what regards biomass, *L. ramada* was the most important species in both areas, representing more than 50% of the catches (in weight). The contribution of *S. senegalensis* was also high, especially in Hortas (29.0%). Fish abundance, both in number and biomass, was higher in Hortas compared to Ponta da Erva mudflat areas.

Mudflats: seasonal variation

The fish assemblages of mudflat areas presented a similar seasonal variation pattern compared to tidal creeks, being

Table 3. Number of individuals and percentage of juveniles per season for the most abundant species captured in the salt marsh creeks and in the mudflat areas at Hortas and Ponta da Erva.

Tableau 3. Nombre d'individus et pourcentage de juvéniles par saison pour les espèces les plus abondantes capturées dans les chenaux de marée et les vasières de Hortas et Ponta da Erva.

	Hortas								Ponta da Erva							
	Creek				Mudflat				Creek				Mudflat			
Species / Season	Aut.	Win.	Spr.	Sum.	Aut.	Win.	Spr.	Sum.	Aut.	Win.	Spr.	Sum.	Aut.	Win.	Spr.	Sum.
Dicentrarchus labrax	0	0	134	5	14	1	748	278	0	0	43	0	3	0	40	26
	-	-	100%	100%	100%	100%	100%	100%	-	-	100%	-	100%	-	100%	100%
Liza ramada	4750	366	10447	10441	67	594	119	32	122	101	3524	263	74	155	99	16
	45%	38%	83%	87%	98%	67%	53%	81%	71%	81%	99%	35%	71%	25%	46%	50%
Pomatoschistus minutus	0	0	0	20	406	735	26	168	2	0	0	8	408	185	191	924
	-	-	-	0%	0%	2%	6%	15%	0%	-	-	0%	1%	0%	12%	18%
Pomatoschistus microps	2015	675	11773	32284	4222	2749	312	687	584	1915	2E+05	2314	1688	760	429	1199
	40%	2%	98%	87%	6%	1%	6%	1%	11%	6%	95%	88%	0%	0%	5%	5%
Sardina pilchardus	53	0	368	5	0	0	0	2	81	0	20315	24	2	1	1	2
	100%	-	100%	100%	-	-	-	100%	100%	-	100%	100%	100%	100%	100%	100%
Solea senegalensis	0	0	0	4	666	99	770	497	0	0	0	0	128	44	91	129
	-	-	-	100%	100%	100%	100%	100%	-	-	-	-	100%	100%	100%	100%

registered the highest diversity and evenness values during spring and summer (Table 2). Diversity values in mudflats were always higher than in the creeks.

The CA ordination diagram showed also a marked seasonal pattern, being the points relative to autumn and winter located in the left edge of the diagram and mainly associated with species such as *P. microps*, *P. minutus* and *L. ramada* (Fig. 6). In this diagram, the points relative to spring and summer periods, mainly located in the right side of the axes origin, were associated with *D. labrax*, *Eengraulis encrasicolus* (Linnaeus, 1758) and *Gobius niger* Linnaeus, 1758 (Fig. 6).

In the mudflat areas, *P. microps* was the most abundant species being the highest values registered during autumn and winter. For both areas, the peak of abundance of *L. ramada* was observed during the winter. As for the creeks, the number of individuals in Hortas was always higher compared to those obtained for Ponta da Erva, with the predominance of juveniles in the former area.

Discussion

The different sampling methods used for salt marsh creeks and adjoining mudflats constrained in part a direct comparison between the data of both habitat types. The same sampling technique could not be applied in both habitat types due to their different characteristics. The fyke net combined with the gill nets and the obligation of the fish to leave the creeks during ebb tides function almost as a non selective sampling method, although species such as *A. anguilla* may avoid the fyke net burrowing in the mud. Unlike the fyke net sampling method, the use of beam-trawl underestimates the abundance of both large and fast swimming individuals, namely mugilids. The higher selectivity of this fishing gear towards benthic fish species was strongly diminished by the shallowness of the water in both sampling sites. Although using different mesh sizes in the salt marsh creeks and in the mudflats, the range of length sizes of the different species sampled in the two habitat types were similar. This fact may be due to the way the net is stretch when the beam-trawl works. These constraints and the distinct sampling years were considered for the selection of the analytical tools to compare the fish assemblages between the two habitat types.

From the 48 species reported in recent studies conducted in the Tejo estuary (Cabral, 1998; Costa et al., 1998) only 27 were present in mudflat areas and 14 in intertidal salt marsh creeks. Lower species richness in the creeks suggested that a limited number of fishes that occurred in the upper part of the estuary use these habitats. The fish species richness in intertidal creeks reported for other European estuarine systems varies considerably. In the North Sea, Cattrijsse et al. (1994) reported the occurrence of 13 fish species in salt marsh creeks of the Westerschelde estuary while Laffaille et al. (1998) found 23 fish species in the creeks of the macrotidal system of Mont-Saint-Michel. Higher species richness (39 species) was obtained for the Cadiz Bay (Drake & Arias 1991). As pointed out by Cattrijsse et al. (1994) these differences may be due to latitudinal effects, but the particularities of both estuarine fish assemblages and salt marsh abiotic and biotic conditions should be the major determinant of species richness. In fact, the areas studied in these last examples, in the Cadiz bay and Mont-Saint-Michel Bay, were subjected to a high marine influence, which surely induces an increase of fish species number.

Regarding the use of the estuary by the different species, the dominance of estuarine resident and marine estuarine-opportunistic species was noted for the creeks fish assemblages in the Tejo, as described for other estuaries (e.g. Rozas, 1995; Kneib, 1997).

In terms of feeding habits, there were some differences in dominant trophic groups in the two habitat types. Although the dominance of benthic macroinvertebrate feeders was registered in both habitat types, the higher preponderance of planktonic feeders in the creeks, also reported for the Forth Estuary (Mathieson et al., 2000), may be associated with the high concentration of zooplankton in the creeks (Salgado, unpublished). The low abundance of piscivorous species also corroborates the findings reported by several authors for other geographical areas (e.g., Cain & Dean, 1976; Miltner et al., 1995). This fact, emphasize the value of this habitat type as refuge against predation by other fish species.

A general characteristic of tidal creek fish assemblages is the dominance, both in number and biomass, by few species (Cain & Dean, 1976; Kneib, 1984; Rakocinski et al., 1992; Cattrijsse et al., 1994). In several studies conducted in European estuaries, *P. microps* (Drake & Arias, 1991; Catrijsse et al., 1994) and *L. ramada* (Drake & Arias, 1991; Laffaille et al., 1998) have been pointed out as the most important fish species in tidal creeks, which is in agreement with the results obtained in the present study.

Working in Mont-Saint-Michel, Laffaille et al. (1998) noticed a low abundance of *P. microps*, but other Gobiidae, such as *P. minutus* and *P. lozanoi* (de Buen, 1923), were present in high densities in tidal creeks. In the Tejo, as in other estuaries (Drake & Arias, 1991; Catrijsse et al., 1994), *P. minutus* was abundant in the salt marshes adjoining areas but not in tidal creeks. This suggests that, depending of the marsh characteristics (e.g. marine influence, hydrodynamic regime) a spatial segregation may be observed in alternative estuarine habitats, such as salt marsh creeks, mudflats or oyster beds.

Drake & Arias (1991), Catrijsse et al. (1994) and Laffaille et al. (1998) found also other fish species, namely

Platichthys flesus (Linnaeus, 1758), *S. solea*, *S. senegalensis* and *D. labrax*, in tidal creeks. In the Tejo, some of these species were particularly abundant in the adjoining mudflat areas, but were absent or only occasionally caught in the creeks. Since the use of tidal creeks can be viewed under a cost-benefit perspective, involving the risk of stranding inside the creek during ebb tide and the gain of foraging opportunities in an area almost free of piscivorous fish species. The lower densities of some benthic invertebrate species inside the salt marsh creeks (Salgado, unpublished), comparing to the nearby mudflat areas, may influence the absence of benthic macroinvertebrate feeders, such as soles (Cabral, 2000).

Despite the similarities in the patterns of variation of temperature and salinity recorded in the two creeks studied, several differences in species abundance were found in the two areas, such as higher abundances of *S. pilchardus* in Ponta da Erva and of *D. labrax*, *P. microps* and *L. ramada* in Hortas creek. These results were also observed for the mudflat areas. Rakocinski et al. (1992) suggested that geomorphologic characteristics of sites are probably the most important factor determining habitat selection by fishes in estuarine tidal creeks. According to Cabral & Costa (2001) the higher abundance of *D. labrax* in Hortas may be due to their preference for sheltered areas, and thus to the better conditions offered by this area. Another factor which might determine this differential abundance distribution is the proximity to a small river (Sorraia River), responsible for the high hydrodynamism within the vicinity of the Ponta da Erva salt marsh creek, which may influence the presence of benthic microalgae and consequently of the species which forage on this food item, such as *L. ramada*.

Seasonal changes in the fish assemblages of tidal creeks reflected mainly the recruitment or pulses of abundance of different species. Some recruits migrate from other estuarine areas, namely *P. microps* (Bouchereau et al., 1993), or from near shore areas, namely *L. ramada* (Almeida, 1996) and *S. pilchardus* (Ré, 1984).

Although capturing a similar range of fish lengths as the fyke net, the beam trawl underestimated the abundance of the smallest size classes and especially of *P. microps*. This fact might be the main reason for the mismatching of the abundance peaks of the different species in the different habitat types. Peaks in the species abundance in the creeks reflect periods of recruitment for the different species, and occurred mainly in spring and summer. Whereas, for some species such as *P. microps* and *L. ramada*, abundance peaks in the mudflats reveal periods of abundance of mature individuals.

The results obtained for the Tejo mudflats showed that diversity and evenness increased in periods of intense recruitment, while in the creeks the pattern of variation was different according to site. Drake & Arias (1991) noted that these indices were higher in winter and late summer and both were significantly correlated with density of resident species.

Most of the species described as using the upper Tejo estuary as nursery areas were absent from the creeks or were only occasional visitors. Nevertheless, those areas were apparently important for *P. microps* and *L. ramada* both as nursery areas and as feeding grounds for the adults (Salgado et al., submitted). For *S. pilchardus*, the importance seems reduced when considering the high densities of larvae and juveniles found at the mouth of the estuary and on the adjacent coastal areas (Ré, 1984; Cabral et al., 2000). However, the analysis of the importance of these habitats for fishes should include the role of the different species as a trophic link between highly productive salt marsh areas and the adjacent estuarine areas or the nearby coastal environments. Laffaille et al. (1998) estimated that in Mont-Saint-Michel, the fish community was responsible for the export of 50 tons (dry weight) of organic matter per year, with mullets responsible for 70% of this transport. The extremely high biomass values of *L. ramada* in the Tejo tidal creeks associated with the foraging behaviour of this species suggests a significant transport of a large amount of organic matter from the tidal creeks towards adjoining estuarine areas or the nearby coastal areas.

In order to understand the role of salt marshes and adjoining mudflats, future studies on trophic interaction between fishes on the salt marsh and on the adjoining mudflats are needed to clarify the importance of these areas for the fish community.

Acknowledgements

This work was possible due to the financial support of the EU through the project EUROSAM (contract ENV4 - CT97 - 0436) and of the Fundação para a Ciência e Tecnologia through the project FESTA (PRAXIS 2/2.1/MAR/1715/95) and the grant PRAXIS XXI BD/3541/97.

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