Original article

The demersal fish assemblage of the coastal area adjacent to the Tagus estuary (Portugal): relationships with environmental conditions

L'assemblage des poissons des zones côtières adjacents à l'estuaire du Tage (Portugal) : relations avec l'environnement

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Abstract

The subtidal fish assemblage of Tagus estuary coastal area was sampled in order to infer about its relationship to environmental conditions and its possible nursery function for marine species. Fish sampling took place between May 2001 and February 2002 with an otter trawl. In addition to fish sampling, a physical, chemical and biological characterization of the water column and bottom sediment was performed. Density and biomass were determined and ecological and feeding guilds assigned to each fish species. Correspondence analysis (CA) was used to determine the spatio-temporal structure of the assemblage and its correlation to environmental variables. A total of 36 fish species were identified. The fish assemblage was dominated by few species, both in terms of density and biomass. The main fish species were *Callionymus lyra*, *Arnoglossus laterna*, *Diplodus bellotti*, *Echiichthys vipera* and *Raja undulata*. Seasonally *Trachurus trachurus*, *Sardina pilchardus* and *Engraulis encrasicolus* were also abundant. Over 50% of the fish caught were juvenile stages. Benthic carnivorous species feeding on invertebrates dominated the assemblage. CA results indicated that distinct fish species occur in the northern and southern areas, although they distance only a few kilometres from each other. Depth and sediment type were the main structuring factors of the fish assemblage. Temperature and salinity showed reduced importance on overall assemblage structure although that may result from the particular climatic regime of the sampling year. The environmental preferences of the most important species are briefly discussed and the importance of integrating various spatial scales in multispecific studies of coastal fish assemblages emphasized. The presence of high densities of marine species juveniles indicates that this area may function as a spring–summer nursery for several species.

Résumé

L'assemblage des poissons de la zone côtière adjacente à l'estuaire du Tage a été prospecté avec un chalut entre mai 2001 et février 2002. En plus de la récolte des poissons, les caractéristiques physiques, chimiques et biologiques du fond et de la colonne d'eau ont été suivies. La densité, la biomasse, l'abondance des juvéniles, les guildes trophiques et écologiques ont été déterminées. L'analyse de correspondance a été utilisée pour analyser la structure spatio-temporelle de l'assemblage des poissons. On a identifié 36 espèces de poissons. L'ensemble est dominé par très peu d'espèces en densité et en biomasse. Les espèces principales sont *Callionymus lyra*, *Arnoglossus laterna*, *Diplodus bellotti*, *Echiichthys vipera* et *Raja undulata*. A certaines périodes de l'année, *Trachurus trachurus*, *Sardina pilchardus* et *Engraulis encrasicolus* étaient aussi abondantes. Plus de 50 % des individus étaient des juvéniles. Les espèces carnivores qui se nourrissent d'invertébrés dominent l'assemblage. Les résultats de l'analyse de correspondance indiquent que différentes espèces de poissons occurrent dans les zones Nord et Sud bien qu'elles soient très proches. La profondeur et le type de sédiment sont les facteurs structurants de la communauté des poissons. La température et la salinité montrent une importance réduite dans toute la structure de la communauté, bien qu'elles puissent résulter du régime climatique particulier de l'année des captures. Les préférences environnementales des espèces les plus importantes sont discutées ainsi que l'importance d'intégrer les plusieurs échelles spatiales dans les études multispécifiques des communautés de poissons

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côtiers. La présence de grandes densités de juvéniles des poissons marins montrent que cette zone peut fonctionner comme une nurserie au printemps été pour plusieurs espèces de poissons.

1. Introduction

Estuaries are far more productive ecosystems than the open sea (Day et al., 1981) and their importance for fish and fisheries has long been recognized all over the world (Blaber et al., 1989; Elliott and Dewailly, 1995). This importance is related to the fact that estuarine fish communities are seasonally dominated by high densities of juvenile stages of marine species (Day et al., 1981). Despite their recognized importance as nursery areas, some controversy exists as to whether or not marine fish species are really dependent on estuaries or just opportunistically using them in order to achieve higher growth rates and a lower exposure to piscivorous predation than found in other inshore coastal areas (Lenanton and Potter, 1987). An increasing body of evidence has been gathered showing that shallow inshore coastal areas may also act as nursery grounds (Lenanton, 1982; Ross et al., 1987; Wright, 1988; Blaber et al., 1995) and can have fish assemblages that include not only species common to both adjacent estuarine and offshore areas, but also characteristic species of their own, not present in nearby marine/estuarine habitats (Blaber et al., 1995). Although recognizing the importance of shallow coastal areas for juvenile fish, recent studies on European coastal waters have frequently used single species approaches and/or neglected less commercially important species (Safran, 1990). As a consequence the contribution of many coastal marine species, some of which important by-catch of fisheries, to shallow water soft-bottom coastal fish assemblages is largely unknown. This is particularly the case of Southern Europe, where few reports include a multispecific approach to fish assemblage (Safran, 1990; Cabral et al., 2000; Letourneur et al., 2001).

Concomitantly, most of the research concerning the relationships between environmental conditions and fish distribution in coastal grounds has been focused on estuaries. Several factors have been reported to influence fish species distribution amongst which depth, salinity, temperature, oxygen concentration, turbidity, sediment characteristics, habitat variability and productivity (Cabral, 2000; Thiel et al., 1995; Marshall and Elliott, 1998; Whitfield, 1999). The fish assemblage of Tagus estuary has been studied last decades and several fish species have been reported to make extensive use of the estuary both in a permanent, seasonal or occasional way (Costa and Bruxelas, 1989; Costa and Cabral, 1999). The available literature on the fish communities of Tagus coastal area suggests that the area is probably important as nursery ground for some marine species which have been reported in decreasing abundances inside the estuary (Cabral et al., 2000). Although this latter study included an extensive sampling programme, with both seasonal and diel coverage through beach seining, it was spatially restricted to an intertidal area located a few kilometres south of Tagus mouth and did not address possible relationships between species abundance and the environmental conditions of the area. The aim of the present work is to analyse the spatial and temporal structure of the fish assemblage of the coastal area adjacent to the Tagus estuary and to evaluate the relative contribution of several environmental variables to the distribution patterns of its main fish species.

2. Materials and methods

2.1. Study area

The Tagus estuary has an area of approximately 320 km^2 of which 40% is intertidal. The Tagus river flow regime presents significant interannual and seasonal variations and is highly dependent on the climatic events occurring in the central part of the Iberian Peninsula (Gaudêncio et al., 1991) and on the outflow rates of several Portuguese and Spanish dams. An annual average flow of 400 m^3 s^{-1} is generally reported with monthly averages fluctuating between 100 and 2200 m^3 s^{-1} (Cabeçadas et al., 2000). The Tagus river outflows from the estuary through a narrow channel 12 km long, 2 km wide and about 30 m deep. Near Cape São Julião and the Bugio island, it opens into a large bay limited on its northern boundary by a mixture of rocky shores and sandy beaches and on its southern boundary by sandy beaches. The bay has two main navigation channels: a deeper canyon in the NE–SW direction and a secondary shallower navigation channel along the northern coastline (Fig. 1). Sediments are essentially sandy with coarser sands occurring in the northern sector whilst offshore mud deposits occur in the outer shelf below 80 m (Dias, 1987; Jouanneau et al., 1998). Tidal regime is primarily semidiurnal with a range of 1.5 m in neap tides and of 3.5 m in spring tides. The tidal currents are highly dependent on the bathymetry of the area with surface currents more intense over the shallower areas than in the main canyon during the flood and an opposite situation during the ebb. The bathymetry and coast morphology also contribute to a situation of tidal reversion near the coast during the ebb due to eddy formation on both sides of the larger canyon (Fortunato et al., 1997). Upwelling favourable winds from northern octants occur in summer (Fiúza et al.,
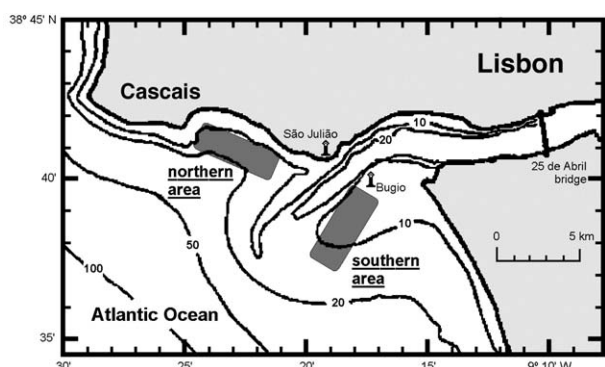
Fig. 1. Location of the sampling sites in the coastal area adjacent to the Tagus estuary with reference to northern and southern trawled areas.

1982) and strong SW winds are common in winter months. The area is relatively protected from the dominant NW swell of the Portuguese coast, although it is exposed to seasonal SW storms (Dias, 1987).

2.2. Sampling techniques

Three samples were taken from each of two areas—located north and south of the main channel of the Tagus estuary—in May 2001, September 2001, November 2001 and February 2002 (Fig. 1). Fish samples were taken with an otter trawl (14.2 m headline, 21.5 m footrope, 50 mm body stretched mesh, 18 mm cod-end stretched mesh). All tows lasted 15 min and were carried out in daylight and in neap tide, at a constant speed of 2.5 knots. Immediately before and after each tow, depth, temperature, salinity and dissolved oxygen concentration were measured with an YSI 600 XLM probe near the bottom (0.5 m over the bottom) and the surface (0.5 m depth). Also before the tow, water transparency was measured with a Secchi disc and 10 l of bottom and surface water were collected with a Wilco horizontal alpha bottle for chlorophyll and suspended solids' determination. Furthermore, a sediment sample was obtained with a van Veen grab and immediately frozen for determination of organic content and grain size composition of sediment.

2.3. Laboratory procedures

All fish were identified, measured (total length with 1 mm precision) and weighed (wet weight with 0.01 g precision). Three water subsamples were filtered (Whatman GF/F filters) for both chlorophyll *a* and total and volatile suspended solids quantification. Chlorophyll extraction was performed in 90% aqueous acetone solution and chlorophyll *a* quantified according to the Lorenzen (1967) spectrophotometric method. Total suspended solids were quantified after oven drying of filters for 24 h at 60 °C. Volatile suspended solids were determined after ignition of filters at 550 °C for 2 h. The Clesceri et al. (1998) formulas were used to quantify total and volatile suspended solids.

Sediment samples were dried at 60 °C and a 100 g subsample wet-sieved through a 0.063 mm mesh sieve and dried.

The remaining sediment was sieved through a four-sieve column. The 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). Organic content of sediment was quantified by the loss on ignition method at 550 °C during 4 h (Heiri et al., 2001) of three 5 g oven dried sediment subsamples.

2.4. Data analysis

In order to evaluate the main spatial and temporal variations in both environmental variables and fish assemblage characteristics (species richness, fish density and biomass), two-factor Model I analyses of variance (ANOVAs) were conducted. Species densities and biomass were defined as the number of individuals per hour (ind. h^{-1}) and as grams of wet weight per hour (g h^{-1}), respectively. The proportion of juveniles assigned to each species was based on the size at first maturity reported in literature (see Appendix A), but as the juvenile density of some species may have been underestimated due to mesh size selection, the ANOVA was not performed on this parameter. The factors used in ANOVA were area (North, South) and sampling date (May, September, November, February). A significance level of 0.05 was considered. If the null hypotheses were rejected a posteriori multiple comparisons were performed using the Tukey honestly significant difference tests (Zar, 1999). Whenever the raw data did not fulfil the ANOVA assumptions of normality and homocedasticity, the data was transformed (Zar, 1999). To compare the fish assemblage functional structure with the one found in the adjacent estuary, the species were classified into two types of guilds: (a) an ecological guild adapted from Lenanton and Potter (1987) that comprehends estuarine resident species (ER), marine species which are predominantly found in estuaries at some stage of their life cycle (ME), species which are frequent in both estuarine and coastal inshore areas (MEI), diadromous migrant species (D) and freshwater species (FW), based on what is known for the Portuguese coast and Tagus estuary; (b) a feeding guild adapted from Elliott and Dewailly (1995) based on studies conducted in the Portuguese coast and in the Tagus area (including unpublished data on stomach contents of the most abundant species in the study area). The food categories used were planktivorous (P), invertebrate feeders (I), piscivorous (F), omnivorous (O) and detritivorous (D).

Correspondence analysis (CA) was used to identify the underlying structure of the fish assemblage and possible relationships of that structure to environmental variables. The CA is an ordination method effective for indirectly

Table 1

Environmental parameters values in Tagus coastal area per area and sampling date. Means and standard deviations of bottom (bot.) and surface (surf.) measurements are presented. CA code refers to the codes used in correspondence analysis diagram

Environmental variable	CA code	Area			Sampling date				
		n	South	North	n	May	September	November	February
Sediment									
Mud (%)	*mud*	11	1.2 ± 0.7	4.4 ± 2.0	6^a	2.1 ± 1.1	3.4 ± 2.7	3.7 ± 2.5	2.3 ± 2.6
Fine sand (%)	*fs*	11	45.7 ± 20.3	83.8 ± 12.6	6^a	68.0 ± 24.6	75.5 ± 23.0	60.4 ± 30.6	58.7 ± 26.6
Medium sand (%)	*ms*	11	50.2 ± 19.4	8.8 ± 12.9	6^a	27.1 ± 26.3	19.1 ± 25.5	31.8 ± 30.7	36.4 ± 28.2
Coarse sand (%)	*cs*	11	2.7 ± 2.2	2.4 ± 0.9	6^a	2.0 ± 0.7	1.7 ± 0.5	3.7 ± 2.8	2.5 ± 1.1
Gravel (%)	*grv*	11	0.1 ± 0.1	0.7 ± 0.7	6^a	0.8 ± 0.9	0.3 ± 0.2	0.5 ± 0.5	0.1 ± 0.1
Organic content (%)	–	11	0.9 ± 0.2	1.9 ± 0.3	6^a	1.4 ± 0.5	1.5 ± 0.6	1.5 ± 0.6	1.3 ± 0.6
Water column									
Depth (m)	*dpth*	24	10.56 ± 2.29	17.60 ± 1.18	12	14.18 ± 4.30	13.71 ± 3.76	14.28 ± 4.32	14.13 ± 4.05
Temperature surf. (°C)	*St*	24	17.16 ± 1.31	17.09 ± 1.06	12	16.98 ± 0.36	18.31 ± 0.36	17.86 ± 0.09	15.34 ± 0.25
Temperature bot. (°C)	*Bt*	24	16.36 ± 1.19	15.97 ± 1.19	12	14.84 ± 0.37	16.54 ± 0.51	17.84 ± 0.11	15.44 ± 0.14
Salinity surf.	*Ss*	24	34.59 ± 0.69	34.50 ± 1.16	12	34.11 ± 0.94	34.28 ± 0.29	33.94 ± 0.42	35.86 ± 0.35
Salinity bot.	*Bs*	24	35.65 ± 0.37	35.71 ± 0.43	12	35.88 ± 0.08	35.17 ± 0.08	35.49 ± 0.13	36.18 ± 0.14
Water transparency (cm)	*wt*	12^b	389 ± 82	491 ± 113	6^b	473 ± 72	343 ± 45	370 ± 73	525 ± 118
Oxygen surf. (mg m^{-3})	*So*	18	8.62 ± 0.69	8.71 ± 0.69	6	9.44 ± 0.21	–	7.85 ± 0.17	8.70 ± 0.13
Oxygen bot. (g m^{-3})	*Bo*	18	8.46 ± 0.67	7.96 ± 0.46	6	8.73 ± 0.55	–	7.52 ± 0.19	8.37 ± 0.21
Total susp. solids surf. (g m^{-3})	*ts*	12	21.8 ± 7.0	22.0 ± 6.1	6	11.7 ± 1.9	25.0 ± 2.6	26.9 ± 2.0	24.0 ± 1.3
Total susp. solids bot. (mg m^{-3})		12^c	25.4 ± 8.0	22.2 ± 5.0	6^c	12.7 ± 2.2	25.0 ± 0.8	27.1 ± 1.3	28.2 ± 5.2
Volatile susp. solids surf. (g m^{-3})	–	12	6.1 ± 1.6	6.0 ± 1.5	6	3.9 ± 0.6	6.4 ± 0.8	7.5 ± 0.7	6.4 ± 0.4
Volatile susp. solids bot. (g m^{-3})	–	12^c	6.5 ± 1.4	5.8 ± 1.1	6^c	4.1 ± 0.4	6.1 ± 0.4	7.3 ± 0.5	6.8 ± 0.6
Chlorophyll *a* surf. (mg m^{-3})	*Sc*	12	3 ± 0.7	3 ± 0.8	6	3 ± 0.0	3 ± 0.8	2 ± 0.7	2 ± 0.8
Chlorophyll *a* bot. (mg m^{-3})	*Bc*	12	2 ± 1.1	1 ± 0.7	6	2 ± 0.5	1 ± 1.0	2 ± 0.5	3 ± 1.6

[a] $n = 4$ in November.

[b] $n = 10$ in North, $n = 4$ in September.

[c] $n = 11$ in South, $n = 5$ in May.

revealing some correlations established between the spatial and temporal structure of communities and environmental factors that might be responsible for that structure (e.g. ter Braak, 1995; Cabral, 2000). The CA was performed on a density data matrix that included all species with >5 individuals captured (20 species, representing 99.2% of total catch) in order to reduce the influence of rare or occasional species. The influence of unusually large catches of some fish species in the CA results was reduced by square-root transformation of data. The set of environmental variables used in the covariable matrix was obtained using the following criteria: (a) all initial and final measurements were averaged, (b) surface and bottom measurements were averaged if correlation coefficient (r) presented values >0.8, and (c) variables that presented high correlation ($r > 0.9$) with other variables were discarded from analysis. Consequently, the variables used were surface and bottom temperature, surface and bottom salinity, surface and bottom dissolved oxygen concentration, surface and bottom chlorophyll *a* concentration, water transparency, total suspended solids and grain size characteristics of sediment, whereas volatile suspended solids and organic content of sediment were excluded from the environmental matrix because they were highly correlated to total suspended solids and to fine sand percentage, respectively. The CA was performed using Canoco 4.0 software (ter Braak, 1988).

3. Results

3.1. Environmental characteristics of the sampling area

Significant temporal and spatial differences were registered in the mean values of the environmental parameters (Tables 1 and 2). Both sampling areas were located on sandy subtidal bottoms. The northern area registered higher depths and higher proportions of fine sand, mud, gravel and organic matter when compared to the southern area where sediment was mainly composed of medium and fine sand. Temperature varied between 14.54 ± 0.12 °C (May-North) and 17.94 ± 0.03 °C (November-South) at bottom, and 15.13 ± 0.14 °C (February-South) and 18.55 ± 0.06 °C (September-South) at surface. All temporal comparisons were highly significant (a posteriori tests: $P < 0.001$). Salinity varied between 35.11 ± 0.04 (September-North) and 36.26 ± 0.01 (February-North) at bottom, and between 33.58 ± 0.97 (May-North) and 36.14 ± 0.19 (February-North) at surface. Bottom salinity differed significantly between all sampling dates but surface salinity values only differed in February (a posteriori tests: $P < 0.001$). Significant differences in bottom temperature and salinity also occurred between areas but were always below 1.00 °C and 1.00, respectively, and no consistent pattern was found towards higher bottom temperatures and/or salinities

Table 2

ANOVA results on spatial and temporal variation in environmental parameters and fish assemblage. "bot." refers to bottom and "surf." to surface measurements

Variable	Area			Date			Area × date			Error	
	df	MS	P	df	MS	P	df	MS	P	df	MS
Sediment											
% mud[a]	1	0.0566	* * *	3	0.0034	ns	3	0.0015	ns	14	0.0019
% fine sand[a]	1	1.4144	* * *	3	0.0385	ns	3	0.0071	ns	14	0.0421
% medium sand[a]	1	0.9541	* * *	3	0.037	ns	3	0.0114	ns	14	0.0397
% coarse sand[a]	1	0.0001	ns	3	0.0028	ns	3	0.0015	ns	14	0.0018
% gravel[a]	1	0.0095	* * *	3	0.0023	ns	3	0.0007	ns	14	0.0007
Organic content[a]	1	0.0089	* * *	3	0.0001	ns	3	0.0000	ns	14	0.0001
Water column											
Depth	1	594.15	* * *	3	0.75	ns	3	0.79	ns	40	3.71
Temperature surf.	1	0.07	ns	3	20.59	* * *	3	0.51	* * *	40	0.05
Temperature bot.	1	1.87	* * *	3	20.83	* * *	3	0.66	* * *	40	0.02
Salinity surf.	1	0.09	ns	3	9.42	* * *	3	1.86	* * *	40	0.21
Salinity bot.	1	0.06	* *	3	2.33	* * *	3	0.07	* * *	40	0.01
Water transparency	1	36053	*	3	32560	* *	3	3471	ns	14	5539
Oxygen surf.	1	0.08	*	2	7.61	* * *	2	0.15	* *	30	0.02
Oxygen bot.	1	2.26	* * *	2	4.66	* * *	2	0.58	* * *	30	0.03
Total susp. solids surf.	1	0.27	ns	3	288.59	* * *	3	9.00	ns	16	3.29
Total susp. solids bot.[b]	1	0.001	ns	3	0.148	* * *	3	0.017	* * *	15	0.001
Volatile susp. solids surf.	1	0.18	ns	3	13.92	* * *	3	1.46	* *	16	0.25
Volatile susp. solids bot.	1	1.49	* *	3	10.40	* * *	3	0.39	*	15	0.10
Chlorophyll *a* surf.[c]	1	0.0001	ns	3	0.09	ns	3	0.135	*	16	0.03
Chlorophyll *a* bot.[c]	1	1.301	* * *	3	0.401	* *	3	0.166	*	16	0.048
Fish assemblage											
Species richness[c]	1	2	* *	3	1.98	* * *	3	0.48	ns	16	0.22
Abundance[c]	1	638	* *	3	227	ns	3	121	ns	16	74
Biomass[c]	1	8248	ns	3	19685	* *	3	11915	*	16	3334

Transformations according to Zar (1999). Level of significance: * * * $P < 0.001$, * * $P < 0.01$, * $P < 0.05$, ns, $P > 0.05$. [a] Arcsin transformation. [b] Logarithm transformation. [c] Square-root transformation.

in any of the areas. Considering the water column, salinity was always higher at bottom denoting brackish water influence in the upper layers whereas surface-to-bottom differences in temperature indicate that thermal stratification occurred in May (mean difference = 2.14 ± 0.41 °C) and September (mean difference = 1.78 ± 0.39 °C) but not in November (mean difference = 0.03 ± 0.18 °C) and February (mean difference = –0.10 ± 0.18 °C) when the water column was disturbed by strong SW winds. Water transparency was significantly higher in February when compared to September and November (a posteriori tests: $P < 0.05$). Oxygen concentrations were consistently above 7 g m^{-3}, and significant differences occurred between sampling dates and between areas with a general trend towards lower bottom oxygen levels in November and in the northern area. Suspended and volatile solids concentrations also presented some spatial and temporal variations being significantly lower in May samples (a posteriori tests: $P < 0.001$). Chlorophyll *a* concentration in the area was low (<4.0 mg m^{-3}). Highly significant spatial differences were nevertheless found in bottom concentrations of northern and southern areas, and between September and February samples (a posteriori tests: $P < 0.001$).

3.2. Fish assemblage structure

A total of 3819 fishes of 18 families and 36 species were collected. The most abundant species were *Callionymus lyra*, *Trachurus trachurus*, *Arnoglossus laterna*, *Diplodus bellotti* and *Echiichthys vipera* (Table 3). In terms of mean density the referred group of species also recorded the highest values of mean abundance, but *A. laterna* assumed higher overall average density than *T. trachurus* (in spite of the lower number of individuals captured) due to its much higher frequency of occurrence. A large fraction of the biomass of the assemblage was also concentrated in a small group of species, namely *Raja undulata*, *C. lyra*, *Diplodus vulgaris* and *D. bellottii* which jointly represented 76% of total biomass caught. *A. laterna*, *Dicologlossa cuneata*, *Trigla lucerna* and *E. vipera* were the most frequent species in the area being present in more than half of the samples. Juvenile life stages comprehended 50.8% of total fish caught (mean = 48 ± 20% of sample catch). Most of the species collected were typically marine species (82.1% of total catch) with only nine known to make significant use of the adjacent estuarine area. In what concerns feeding preferences, invertebrates and bottom-associated fish feeders dominated the assemblage

Table 3

The fish assemblage of the coastal area adjacent to Tagus estuary. Ecologic and feeding guild classification, number of individual captured (*N*), frequency of occurrence (*FO*), mean density (*D*), mean biomass (*B*), and percentage juvenile stages (% Juv) are shown along with temporal and spatial variations in density expressed as mean density by sampling date and area, respectively. "CA code" refers to the codes used in correspondence analysis diagram and "?" to lack of length at first maturity data for the species

Species	CA code	Eco. Guild	Feed. Guild	*N*	*FO* (%)	*D* (ind. h⁻¹)	*B* (g h⁻¹)	Season (ind. h⁻¹)				Area (ind. h⁻¹)		Juveniles (ind. h⁻¹)				% Juv
								May	Sep	Nov	Feb	South	North	May	Sep	Nov	Feb	
Callionymus lyra	Cl	M	I	1298	50	196	7461	79	390	148	165	–	391	1	108	59	59	27
Trachurus trachurus	Tt	M	P, I	696	42	60	188	200	22	–	19	100	20	200	21	–	19	100
Arnoglossus laterna	Al	M	I, F	551	83	83	639	33	188	57	55	45	121	28	135	46	45	77
Diplodus bellottii	Db	MEI	O	377	50	51	2952	44	43	–	116	31	70	11	–	–	16	16
Echiichthys vipera	Ev	M	I, F	143	54	21	245	11	35	4	32	40	1	9	11	3	19	56
Sardina pilchardus	Sp	MEI	P, I	111	29	18	147	2	3	–	66	33	2	–	1	–	64	91
Diplodus vulgaris	Dv	MEI	O	109	29	14	3352	15	40	–	1	–	28	2	3	–	1	12
Dicologlossa cuneata	Dc	M	I	105	75	15	973	10	35	4	9	11	19	1	1	–	1	5
Buglossidium luteum	Bl	M	I	82	50	11	103	11	15	2	15	4	17	0	–	–	–	1
Engraulis encrasicolus	Ee	MEI	P	72	8	12	94	–	–	–	47	24	–	–	–	–	28	60
Spondyliosoma cantharus	Sc	M	O	64	25	11	923	1	41	1	–	0	21	1	31	1	–	77
Trigla lucerna	Tl	M	I, F	59	75	9	915	2	24	7	6	13	6	2	24	7	6	100
Raja undulata	Ru	M	I	28	33	4	8746	1	5	3	8	8	1	–	–	–	–	?
Trisopterus luscus	Tlu	M	I, F	20	8	2	3	6	–	–	–	3	0	6	–	–	–	100
Solea lascaris	Sl	M	I	15	33	2	154	1	1	1	7	4	–	1	–	–	5	73
Mullus surmuletus	Ms	M	I	15	25	2	135	1	7	1	1	4	1	–	6	–	1	67
Boops boops	Bb	M	O	14	25	2	303	2	5	–	1	1	3	1	–	–	–	29
Merluccius merluccius	Mm	M	F	11	17	1	277	2	4	–	–	–	3	2	4	–	–	100
Aspitrigla obscura	Ao	M	I	10	13	2	32	–	7	–	–	1	2	–	–	–	–	?
Pomatoschistus minutus	Pmi	MEI	I	8	25	1	2	0	3	1	1	1	1	–	1	–	–	13
Psetta maxima	–	M	I, F	4	17	1	203	1	1	–	1	1	1	–	1	–	1	50
Scophthalmus rhombus	–	M	I, F	4	13	0	254	1	1	–	1	1	–	0	–	–	1	50
Solea senegalensis	–	ME	I	3	13	0	107	1	–	–	1	0	0	–	–	–	–	0
Callionymus reticulatus	–	M	I	3	13	0	2	–	1	–	1	1	–	–	–	–	–	?
Spicara maena	–	M	P	3	8	1	34	–	2	–	–	–	1	–	–	–	–	0
Liza ramada	–	D	D, P	2	8	0	68	–	–	–	1	1	–	–	–	–	–	0
Solea solea	–	ME	I	2	8	0	65	0	1	–	–	–	0	0	1	–	–	100
Raja clavata	–	M	I	2	4	0	409	1	–	–	–	0	–	0	–	–	–	50
Pollachius pollachius	–	M	F	1	4	0	137	–	1	–	–	–	0	–	–	–	–	?
Diplodus sargus	–	M	O	1	4	0	128	–	1	–	–	–	0	–	–	–	–	0
Liza aurata	–	ME	I	1	4	0	71	–	–	–	1	0	–	–	–	–	1	100
Scomber scombrus	–	M	I, F	1	4	0	59	–	1	–	–	–	0	–	–	–	–	0
Raja montagui	–	M	I	1	4	0	35	–	1	–	–	0	–	–	1	–	–	100
Pagellus acarne	–	M	O	1	4	0	7	–	–	–	1	–	0	–	–	–	1	100
Arnoglossus imperialis	–	M	I, F	1	4	0	5	–	1	–	–	–	0	–	–	–	–	?
Pagrus auriga	–	M	I	1	4	0	3	–	–	–	1	–	0	–	–	–	–	?

comprising about 90% of the species sampled. However, the few omnivorous and strictly planktivorous species were important in terms of abundance.

3.3. Temporal and spatial trends

The Anova results on fish parameters provide some insight on temporal and spatial variability (Table 2). The two compared areas registered significant differences in fish density and species richness, with a trend towards the occurrence of a higher number of species and higher densities in the samples collected in the northern area (Table 4). Species richness also significantly differed between sampling dates with November samples registering a lower species number than the rest of the samples. A similar temporal trend was observed in biomass (a posteriori test: $P < 0.05$) (Table 4).

In what concerns variations in individual species density, *C. lyra* and *D. vulgaris* individuals were only sampled in the northern area while *E. vipera*, *Sardina pilchardus* and *Engraulis encrasicolus* were mostly sampled in the southern area (Table 3). *C. lyra* and *A. laterna* were recorded in moderate to high densities in practically all sampling dates but five other abundant species presented density peaks, namely *T. trachurus* in May, *Spondyliosoma cantharus* in September, *D. bellotti*, *S. pilchardus* and *E. encrasicolus* in February (Table 3). High densities of juveniles were recorded for *A. laterna* and *C. lyra* and also for commercially important species such as *T. trachurus*, *E. encrasicolus*, *S. pilchar-*

Table 4
Number of species, density (total, adult and juvenile) and biomass per area and sampling date. Mean values and standard deviations are presented. Number in parentheses refers to species richness. *n* (area) = 12 and *n* (date) = 6

	Number of species	Density (ind. h^{-1})			Biomass (g h^{-1})
		Total	Adults	Juveniles	
Area					
South	7.0 ± 3.6 (25)	329 ± 416	91 ± 122	228 ± 365	24 168 ± 26 083
North	10.3 ± 4.3 (28)	712 ± 496	437 ± 300	270 ± 206	34 295 ± 29 820
Sampling date					
May	9.3 ± 3.6 (23)	423 ± 457	156 ± 154	266 ± 489	16 759 ± 9689
September	11.5 ± 5.1 (28)	875 ± 670	511 ± 430	350 ± 253	55 469 ± 33 648
November	4.2 ± 1.5 (11)	227 ± 300	109 ± 158	115 ± 144	10 498 ± 11 216
February	9.7 ± 2.3 (24)	556 ± 287	280 ± 158	266 ± 173	34 200 ± 27 582

dus, *S. cantharus* and *T. lucerna*. It is noticeable that *D. bellotti* did not present high abundances of juvenile stages regardless of the high abundance of the adult stages in Tagus coastal area.

The first three ordination axes of CA explained 67.1% of density data, with the first two axes representing by themselves about 50.2%. The first ordination axis separated the northern samples from the southern samples (Fig. 2). In the diagram species like *C. lyra*, *S. cantharus*, *D. vulgaris* and *Merluccius merluccius* show a preferential distribution near most of the northern area samples, while *R. undulata*, *E. vipera*, *S. pilchardus*, *E. encrasicolus* and *Solea lascaris*
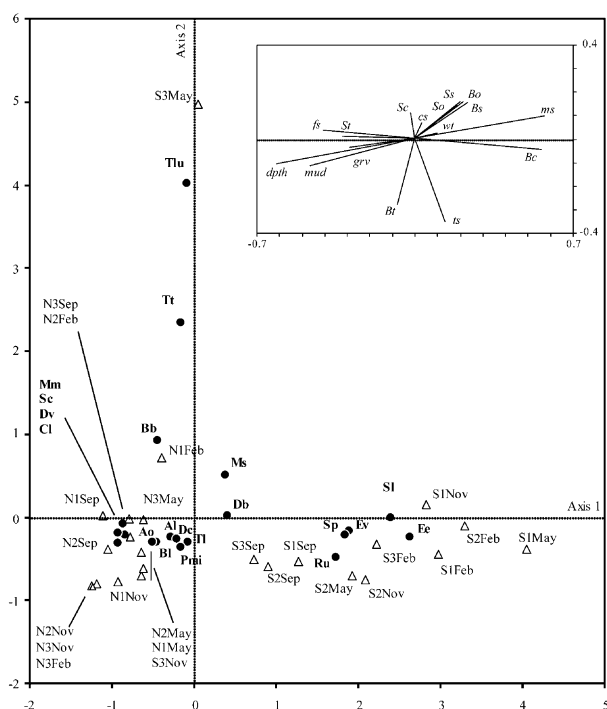

Fig. 2. CA ordination diagram relative to density data (20 species, 99.2% of total catch). The first two ordination axes represent 50.2% of total species variance. The eigenvalues of axes 1 and 2 are 0.49 and 0.36, respectively. The species–environment correlation of axes 1 and 2 are 0.97 and 0.95, respectively. Black dots refer to species (see Table 3 for species codes), open triangles to samples (sample-month). Inset graph presents biplot scores of environmental variables on the two ordination axes (see Table 1 for environmental parameters codes).

occur nearer to southern samples. On the contrary, other abundant species like *A. laterna*, *D. bellotti* or *D. cuneata* bear little association to any of these two groups being located near the origin of the diagram. *T. trachurus*, *Trisopterus luscus* and sample S3-May are located along the second ordination axis in a distant diagram position because this sample accounted for over 90% of these species captures. Another atypical position is obtained by sample S3-November (that registered four species in low densities, one of them—*S. cantharus*—that showed strong preference to the northern area in the rest of the samples) and by the sample N1-February (that registered relatively high numbers of *T. trachurus* and *D. bellotti* when compared to other northern samples). It is also noticeable that the southern group of samples presents a higher dispersion in ordination scores along the first axis than the northern group. This is due to higher variability in species caught in the southern area, where only a few species—*E. vipera*, *S. lascaris* and *R. undulata*—showed a consistent presence throughout the year. As to indirect gradient analysis results, 72.8% of the density matrix species–environment relation was explained in the first three CA axes, with the first two accounting for 54.9% of the variability. Despite the statistically significant differences between areas and sampling dates (Table 2), high correlations (>|0.70|) of environmental variables with ordination scores only occurred in the first axis, and were mainly related to geographical variables like depth and sediment grain size composition or to chlorophyll *a* concentration. Correlations of environmental variables with the second axis were all <|0.50|.

4. Discussion

4.1. Global patterns

Although the fishing gear used may have caused some underestimation of flatfish density and biomass estimates (Kuipers et al., 1992), it is not expected to have had a significant effect on the overall structure of the community. In fact, the otter trawl is considered a useful gear for community approaches to demersal fish assemblages providing good quantitative data on both demersal and benthic fish species

Table 5
Main species (in decreasing order of importance) of the soft-bottom fish assemblage of Tagus coastal area. Note that Cabral et al. (2000) data are based on beach seine catches

Rank	Cabral et al. (2000)	This study	
	Southern intertidal	Southern subtidal	Northern subtidal
1	*Trachurus trachurus*	*Trachurus trachurus*	*Callionymus lyra*
2	*Scomber japonicus*	*Arnoglossus laterna*	*Arnoglossus laterna*
3	*Sardina pilchardus*	*Echiichthys vipera*	*Diplodus bellottii*
4	*Atherina presbyter*	*Engraulis encrasicolus*	*Diplodus vulgaris*
5	*Trisopterus luscus*	*Sardina pilchardus*	*Spondyliosoma cantharus*
6	*Buglossidium luteum*	*Diplodus bellottii*	*Trachurus trachurus*
7	*Diplodus bellotti*	*Trigla lucerna*	*Dicologlossa cuneata*
8	*Echiichthys vipera*	*Buglossidium luteum*	*Buglossidium luteum*
9	*Boops boops*	*Dicologlossa cuneata*	*Trigla lucerna*
10	*Arnoglossus laterna*	*Trisopterus luscus*	*Boops boops*

(Hemingway and Elliott, 2002). However, fast species like the mackerels (He, 1993) and species with a wider distribution in the water column and/or the intertidal areas like *Atherina presbyter*, that were amongst the dominant species of Cabral et al. (2000) work (Table 5), were practically absent from this study. The absence of these two species from trawl catches may be due to gear selectivity or, more likely, may be related to a more pelagic and/or intertidal distribution. In fact, the beach seine technique used by Cabral et al. (2000) tends to sample most of the water column in mostly intertidal grounds while the otter trawl operates near the bottom in subtidal areas relatively distant from the coast. It should also be noticed that the densities of the smaller individuals of some species are likely to have been underestimated due to trawl mesh selectivity. An analysis of the length-frequency of captures of the 10 most captured species indicated that should be the case of *Callionymus lyra* and *Buglossidium luteum (unpublished data)* but is not expected to have occurred in the remaining species (e.g. *Diplodus* juveniles have been captured in large quantities with the same gear and mesh size inside Tagus estuary).

The subtidal fish assemblage of Tagus coastal area is dominated by a reduced number of species some of which present high fluctuations in densities and biomass throughout the year. A similar structure has been reported in several shallow inshore coastal areas from different parts of the world (e.g. Ross et al., 1987; Wright, 1988; Safran, 1990; Clark et al., 1994; Letourneur et al., 2001). The dominant species in Tagus coastal zone are *C. lyra*, *Arnoglossus laterna*, *Echiichthys vipera* and *Diplodus bellottii*, although in some periods of the year, *Trachurus trachurus*, *Sardina pilchardus* and *Engraulis encrasicolus* present relatively high densities. In terms of biomass, *Raja undulata* and *C. lyra* assume the dominance despite the first species low number of individuals captured. As to juvenile composition, the fish assemblage of Tagus coastal waters is very different from the one that uses the nearby Tagus estuary. Our results indicate that significant densities of less commercially important species juveniles like *C. lyra* and *A. laterna* are present in the area throughout most of the year which may indicate that these two species spawn in the area or in nearby

coastal grounds. The presence in some sampling dates of relatively high abundances of juveniles of commercially important species namely *T. trachurus*, *S. pilchardus*, *Spondyliosoma cantharus*, *E. encrasicolus*, *Trisopterus luscus* and *Trigla lucerna* further indicates that this area may be an important nursery ground for these species. As *Dicentrarchus labrax*, *Solea solea* and *Solea senegalensis* are the main species that use Tagus estuary as nursery ground (Costa and Cabral, 1999), a significantly different nursery role is carried out by the two adjacent systems. The use of the coastal area by a distinct marine juvenile assemblage is probably related to the fact that it is a relatively shallow water habitat, receiving considerable productivity inputs from the adjacent estuary and where more stable environmental conditions induce lower degrees of environmental stress on marine fish juveniles comparatively to the adjacent estuarine habitat. This idea is strengthened by the fact that most of the species in the area do not make significant use of the adjacent estuary. One such case is *T. trachurus* whose juveniles are known to form nearshore aggregations (Borges, 1984). Furthermore, the presence of *S. pilchardus* in the area could be related to the fact that estuarine plumes tend to concentrate zooplankton and larval fish forms (Kingsford and Suthers, 1994), a phenomenon that may be enhanced by ebb tide surface eddy formation in the southern sandbanks (Fortunato et al., 1997). Other evidence comes from the increase in species richness in spring to late summer samples. This increase is probably associated to offshore–onshore movements of marine species towards shallower and more productive coastal systems, a similar situation to the reported by Fonds (1983) in the Wadden Sea.

Most of the demersal species of Tagus coastal area feed on infauna and epifauna, or bottom-associated fish. A similar situation has been reported in Tagus estuary and in other estuarine systems (Elliott et al., 2002) and in the French Mediterranean (Letourneur et al., 2001) where the demersal fish assemblage feeds primarily on benthic macrofauna. However, it is noticeable that, contrary to what happens inside Tagus estuary, the Mugilidae family assumes reduced importance in the coastal area, both in the subtidal and intertidal (Cabral et al., 2000). This indicates an important

trophic difference between the two adjacent locations since mullets assume the detritivorous/benthic microalgae trophic link of Tagus estuarine fish assemblage (Almeida et al., 1993). Furthermore, despite the reduced importance in terms of number of species, planktivorous species such as *S. pilchardus*, *E. encrasicolus* and juvenile stages of *T. trachurus* were abundant in February and May. Since *S. pilchardus* is a pelagic species, planktivory might in fact have assumed high seasonal importance in the system if the whole water column was being considered, a fact that occurs in the coastal intertidal areas (Cabral et al., 2000) and that is less pronounced in the upper areas of Tagus estuary (Moreira et al., 1992).

4.2. Spatio-temporal patterns: relationships to environmental conditions

The results of the present study allow, when analysed in conjunction with Cabral et al. (2000) beach seine data, a comprehensive view of both subtidal and intertidal fish assemblages of Tagus coastal area (Table 5). The overall results indicate that at least 64 fish species occur in the area, a number that would most probably increase if the pelagic subtidal area and the northern rocky shore were sampled. Furthermore, the results of the present study show that important changes in fish assemblage structure occur between sites located only a few kilometres apart. Related to this is the fact that the CA plot separated the northern and southern samples revealing the spatial component as the main environmental gradient in species densities, even if high temporal fluctuations in some fish species abundance occur. Furthermore, the CA results indicate that a substantial part of the variability of the fish assemblage may be explained by the studied environmental variables. The most important environmental conditions would then be depth, sediment characteristics and chlorophyll *a* concentration. However, other environmental variables, biological interactions or a combination of both should also be taken into account when indirectly analysing CA results on fish assemblages and species preferences. In fact, despite the high correlation of depth with the first axis of the CA diagrams (Fig. 2), this variable may only work geographically (since the differences in depth between northern and southern areas—about 10 m—do not appear to be biologically significant) or, on the contrary, be expressing the influence of some underlying correlated variables. One such variable may be the degree of proximity to the northern rocky shores. The proximity to rocky shores not only increases habitat heterogeneity creating a wider and distinct potential diversity of niches available for fish species but can also modify the macrofauna distribution and abundance in adjacent sandy-bottoms where reef-associated fish species are often seen to forage (Henriques et al., 1999; Barros et al., 2001) leading to significantly different fish assemblages. A possible evidence of the importance of this variable can be found in the highly significant increase in mean species number in samples collected in the northern area and in the strong association to this area of *Diplodus vulgaris* and *S. cantharus*, that are frequently caught on areas

of convergence of sand, gravel and rocky substrates (Gonçalves and Erzini, 1998). However, quite a different sampling design would be needed to test alternative hypotheses like for example that the degree of exposure to wind, swell or to estuarine outflow might also be determinant. The presence of a small percentage of shell debris in the bottom samples of the northern area (up to 2.5%) may be related to the death of reef-associated molluscs redistributed by local currents and wave action (Barros et al., 2001) and may be seen as evidence of reef influence on adjacent soft-bottom areas. Accordingly, the proximity to the rocky environment of the northern coastline should play a more important role in the species distribution than depth. A similar situation may have occurred with the correlation observed between the bottom chlorophyll *a* concentration and the first axis of the CA plot (Fig. 2). Once more, although statistically significant, the reduced range of variation of chlorophyll *a* concentration (ca. 4 mg m^{-3}) should not present a direct biological significance to the spatial structure of the fish assemblage. Conversely, the CA first axis presents high correlation with type of sand namely with the high percentage of soft sand in northern samples and the high percentage of medium grain sand in southern samples. In contrast to depth and chlorophyll *a* concentration, sediment composition may in fact be structural in the fish assemblage since, as suggested by the CA analysis, *E. vipera* abundance has been found to be positively correlated to medium grain size sandy bottoms in the North Sea (Creutzberg and Witte, 1989). Accordingly, *A. laterna* and *B. luteum* that take a not so high association to the first axis may be expressing the independence of their distribution in relation to sediment type (Amezcua and Nash, 2001). In what concerns *C. lyra*, its distribution is not known to be dependent on bottom grain size (van der Veer et al., 1990), being found both in muddy and sandy substrates (King et al., 1994). Accordingly, more probable causes to the preferential distribution of this species in the northern area are differences in substrate food availability between the two areas (unpublished data), the opportunistic feeding on rocky shore mussel beds epifauna (López-Jamar et al., 1984; Fernández et al., 1995) or the preference for more sheltered areas since the northern area of the Tagus mouth registers lower tidal currents speeds (Fortunato et al., 1997) and is also less exposed to the dominant winds due to northward presence of mountainous formations. As to *D. bellotti*, it is a species with southern affinities that has been extending northwards its distribution range (Cabral et al., 2001). In the Tagus coastal area, it is commonly found both in the northern and southern areas, showing no abundance trend within the range of the measured environmental variables (Fig. 2).

It is also noticeable that CA axes presented reduced correlations with environmental parameters even if they registered considerable fluctuations throughout the year. Regarding that salinity and temperature frequently appointed as important factors influencing species distribution in coastal and estuarine ecosystems (Fonds, 1983; Thiel et al., 1995), the absence of a recognizable temporal pattern in the dia-

grams may be related either to sampling strategy limitations or to the particular winter climatic situation that took place during the sampling events. Dry periods are known to occur frequently in the Iberian Peninsula and in 2001/2002 reflected themselves in smaller salinity and temperature variations than it would be expected based on the typically seasonal outflow regime of Tagus estuary and on the proximity of the sampling areas to the estuary mouth. Evidence of the possible effect of a year's specific climatic regime in community structure was obtained during preliminary sampling activities carried out in the 2000/2001 winter when salinities and water temperatures in the southern area were frequently below 30 and 15 °C, respectively, and appreciable densities of juvenile *Argyrosomus regius* were recorded. It is significant that in the following winter, *A. regius* juveniles were not captured since the use of the coastal areas near estuaries as overwintering areas by this species has been related to winter reduction in estuarine temperatures (Quéro and Vayne, 1987) and *A. regius* juveniles were very abundant throughout 2002 inside Tagus estuary (unpublished data). Regarding these facts, the importance of typically seasonal environmental variables like temperature and salinity to fish assemblage structure in this area should be interpreted with caution until a more comprehensive annual and seasonal sampling scheme can be accomplished.

5. Conclusion

The subtidal fish assemblage of Tagus estuary coastal area is dominated by a reduced number of typically marine species. However, significant immigration movements occur from offshore into this coastal area, especially during spring and summer. The number and species of juvenile life stages present in the area indicates that it may be used by some marine species as a nursery area. When compared to Tagus estuary, this nursery function is used by a different array of marine species. Most of the variability in the fish assemblage can be explained by typical geographical variables like depth and sediment characteristics although these may be correlated to the proximity to northern rocky shores or the degree of exposure to winds and swell. Consequently, the possible existence along estuarine-coastal gradients of structurally and functionally distinct fish assemblages should be taken into account when developing management strategies for coastal ecosystems.

Acknowledgements

Appendix A

Size at first maturity considered in juvenile stage quantification. "Fishbase calculation" refers to the usage of site www.fishbase.org for determination of length at first maturity based on growth parameters for the species; "average of sexes" refers to average of female and male lengths; "combined" refers to overall size at first maturity determined by authors based on both sexes

Species	Length (mm)	Source	Type of data
Arnoglossus imperialis	–	–	–
Arnoglossus laterna	109	Deniel (1984)	Females
Aspitrigla obscura	–	–	–
Boops boops	143	Gordo (1992)	Average of sexes
Buglossidium luteum	80	Deniel (1984)	Females
Callionymus lyra	122	King et al. (1994)	Average of sexes
Callionymus reticulatus	–	–	–
Diplodus bellottii	117	Santos et al. (1998)	Average of sexes
Dicologlossa cuneata	170	Dinis (1986)	Females
Diplodus sargus	173	Erzini et al. (2001)	Combined
Diplodus vulgaris	172	Erzini et al. (2001)	Combined
Engraulis encrasicolus	111	Millan (1999)	Average
Echiichthys vipera	95	Creutzberg and Witte (1989)	Fishbase calculation
Liza aurata	300	Almeida (1996)	Females
Liza ramada	240	Almeida (1996)	Females
Merluccius merluccius	422	Lucio et al. (1998)	Combined
Mullus surmuletus	175	Quéro (1984)	Average of sexes
Pagellus acarne	177	Erzini et al. (2001)	Combined
Pagrus auriga	–	–	–
Psetta maxima	310	Quéro (1984)	Average of sexes
Pomatoschistus minutus	50	Arruda et al. (1993)	Average of sexes
Pollachius pollachius	–	–	–
Raja clavata	725	Quéro (1984)	Average of sexes
Raja montagui	625	Quéro (1984)	Average of sexes
Raja undulata	–	–	–
Spondyliosoma cantharus	185	Erzini et al. (2001)	Combined
Solea lascaris	219	Gomes (2000)	Females
Spicara maena	149	Dulčić et al. (2000)	Fishbase calculation
Sardina pilchardus	155	Figueiredo and Santos (1988)	Both sexes
Scophthalmus rhombus	310	Quéro (1984)	Average of sexes
Scomber scombrus	245	Regule and Cuadros (1987)	Average of sexes
Solea senegalensis	300	Dinis (1986)	Females
Solea solea	320	Dinis (1986)	Females
Trigla lucerna	378	Baron (1985)	Average of sexes
Trisopterus luscus	190	Sobral (1985)	Average of sexes
Trachurus trachurus	225	Borges and Gordo (1991)	Females

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