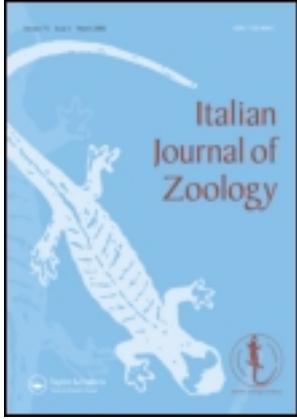


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Fish assemblages in different littoral habitat types of a hypersaline coastal lagoon (Mar Menor, Mediterranean Sea)

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Abstract

The fish community that inhabits shallow littoral areas of the Mar Menor coastal lagoon was studied seasonally. Three different habitat types were compared: deep sandy habitats, vegetated habitats and shallow muddy habitats. The results indicated that the dominant fish families in the lagoon were Mugilidae, Gobiidae, Sparidae and Atherinidae. In general, vegetated habitats and shallow muddy habitats showed higher fish abundance, biomass and fish diversity than deep sandy habitats. Moreover, fish community structure differed significantly among habitats. Vegetated habitats and shallow muddy habitats seems to play an important nursery role, mainly for marine migrant species of the Mugilidae and Sparidae families, and constituted essential habitats for species of conservationist interest such *Aphanius iberus* and *Syngnathus abaster*. Deep sandy habitats were dominated by the resident goby *Pomatoschistus marmoratus*. These habitat-related differences are probably related to variations in structural complexity.

Keywords: *Coastal lagoon, shallow habitats, fish fauna, endangered species, recruitment*

Introduction

Shallow inshore areas of coastal lagoons and estuaries are usually among those marine habitats with the highest biological productivity (Day et al. 1989), that provide suitable habitats for numerous fish species and function as nursery grounds for the early life stages of many fishes (Elliott et al. 2007). Despite their importance, transitional waters are among the most vulnerable aquatic environments in the world, supporting considerable anthropogenic pressures that usually lead to changes in their biological well-being (Vasconcelos et al. 2007; Courrat et al. 2009).

Fish assemblages in these systems change both at temporal and spatial scales in relation to environmental parameters, such as water chemical-physical factors like temperature and salinity (Drake et al. 2002; Akin et al. 2005; Koutrakis et al. 2005; Pombo et al. 2005; Maci & Basset 2009) or parameters related to habitat structure like depth, substrate type and submerged vegetation coverage (Franco et al. 2006; Ribeiro et al. 2006; França et al. 2009).

In addition, fish communities show seasonal shifts in their structure and composition as a result of species-specific differences during recruitment periods and the inward migration timing of larvae or juvenile individuals (Rountree & Able 2007).

Therefore, information about the differential use of shallow habitats by fish fauna in transitional water ecosystems is a critical ecosystem management issue (Franco et al. 2006; França et al. 2009).

The Mar Menor coastal lagoon is one of the largest coastal lagoons in the Mediterranean Sea. Its coastline is densely populated and impacted by a variety of human pressures such as urban development, the construction of marinas and creation of artificial beaches. Nevertheless, the importance of the lagoon and its wetlands (saltpans and natural saltmarshes) in terms of biodiversity has been recognised in numerous national and international protection schemes. The lagoon maintains a diverse fish community due to its environmental heterogeneity: unvegetated sandy and muddy bottoms, rocky bottoms and seagrass beds of *Cymodocea nodosa* (Ucria) Ascherson

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and *Ruppia cirrhosa* (Petagna) Grande (Pérez-Ruzafa et al. 2005; Oliva-Paterna et al. 2006). It also supports important commercial fisheries, primarily Anguillidae (*Anguilla anguilla*), Sparidae (*Sparus aurata* and *Diplodus* spp.), Mugilidae (*Mugil cephalus* and *Liza* spp.) and Atherinidae (*Atherina boyeri*) (Pérez-Ruzafa et al. 2005; Andreu-Soler et al. 2006).

Despite the ecological and economic importance of this biological assemblage, little is known about the temporal and spatial patterns of fish populations in the shallow littoral areas of the lagoon, and their importance as nursery grounds for species of commercial and conservationist interest. Therefore, this study aims to assess the value of the different littoral habitat types in the Mar Menor by determining spatial patterns of habitat use by fish assemblages.

The specific aims of this study were: 1) to identify the main habitat types, based on their environmental characteristics, of the shallow littoral areas of the Mar Menor, 2) to compare the fish community structure, the abundance and biomass of the dominant fish species in these habitats.

Materials and methods

Study area

The Mar Menor is a restricted hypersaline coastal lagoon located in a semiarid region in the southeast of the Iberian Peninsula (Figure 1). It has an area of 135 km² and an average depth of 3.6 m. It is separated from the Mediterranean Sea by a 22 km-long sand bar called La Manga with three inlets connecting it with the open sea. The lagoon displays a salinity range of 39–45 and temperature varies from 10°C in

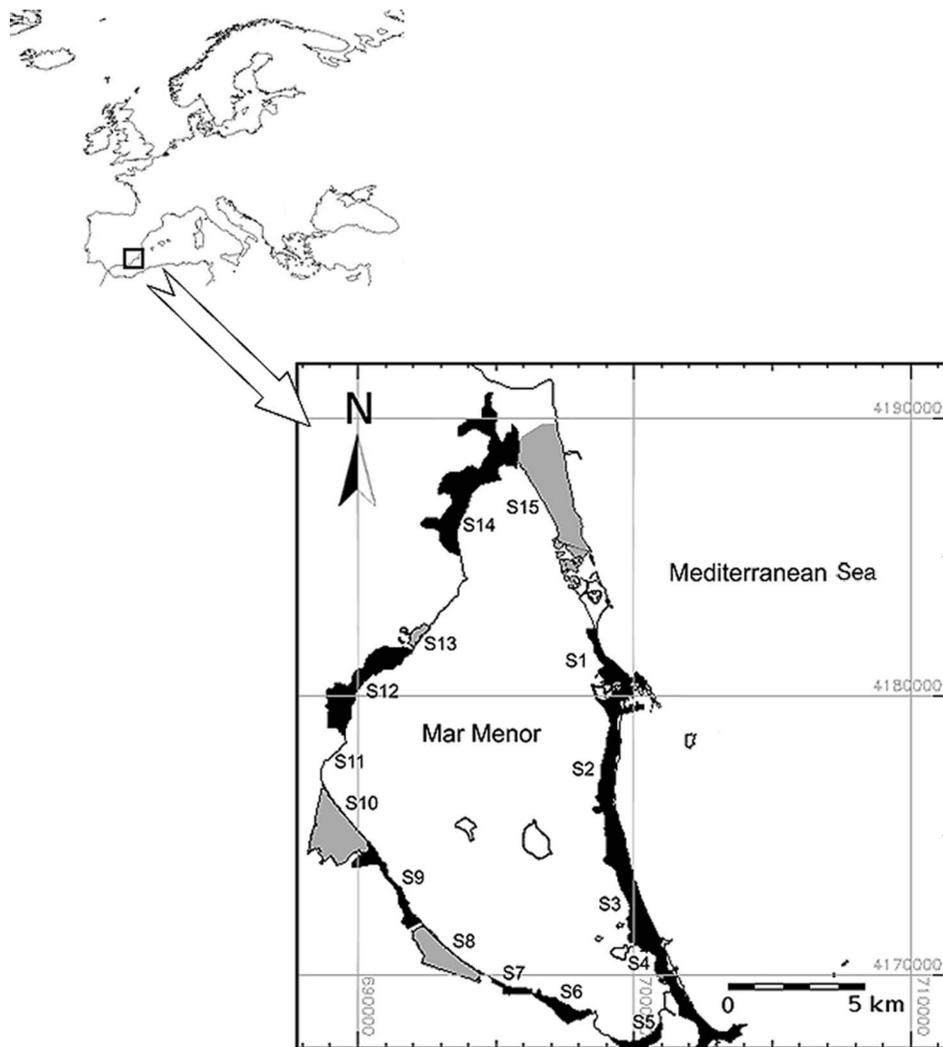


Figure 1. Location of the Mar Menor coastal lagoon and distribution of sampling sites. Grey areas represent wetlands (salt pans and natural salt marshes) and black areas are urbanised areas with residential use.

winter to 32°C in summer. Its bottom is principally covered by dense meadows of the invasive macroalga *Caulerpa prolifera* (Forsk.) Lamouroux, although the shallowest areas are covered by scarce patches of the phanerogams *C. nodosa* and *R. cirrhosa* (Lloret et al. 2005; Pérez-Ruzafa et al. 2005).

Shallow littoral areas (maximum depth < 1 m) of the lagoon are mainly characterised by soft substrates (muddy and sandy bottoms) and isolated patches of submerged vegetation.

Sampling methods

Sampling was carried out on a seasonal basis, during the summer (July) and autumn (October) of 2003, and the winter (February) and spring (May) of 2004. A total of 15 sampling sites were selected in the shallow littoral areas of the lagoon (Figure 1). Samples were collected using a 10 m-long beach seine (2 mm mesh size), which allowed the capture of juvenile fishes and adults of small sized species. Six replicates were collected during every sampling period at each sampling site by hauling 20 m reaches of shoreline at each replicate. The area covered by each haul was approximately 160 m² (standardised hauled area per sampling site = 960 m²), with a total number of 263 samples taken (in some cases it was not possible to perform six replicates at each sampling site due to adverse weather conditions or massive proliferation of filamentous algae).

Fish were anaesthetised with benzocaine, fixed in neutralised formaldehyde (10%) and identified at species level in the laboratory.

The abundance and biomass of fish species at each replicate were recorded and expressed as number of individuals per 100 m² and grams of fish biomass per 100 m², respectively.

Habitat structure was characterised by five environmental variables (quantified in each replicate of every sampling site): water depth (cm), submerged vegetation cover (%), submerged vegetation density, substrate size and substrate heterogeneity. Submerged vegetation cover and submerged vegetation density were assessed visually; the former recorded as the percentage of the area covered by submerged vegetation in each replicate and the latter as an ordinate categorical variable from 0 (low meadow density) to 5 (high meadow density). Substrate particle size was classified according to Bain (1999) [mud (1), sand (2), gravel (3), pebble (4) or boulder (5)] and was assessed by making 10 visual designations at each reach. The substrate particle size and substrate particle heterogeneity were calculated as the average value and the standard deviation at each sampling site, respectively.

Statistical analysis

Sampling sites were ordered using non-metrical multidimensional scaling (MDS), which was applied to a resemblance matrix based on the Euclidean distance generated on the mean normalised values of the environmental variables at each sampling site. Sampling sites were classified into different habitat types by hierarchical cluster analysis (Euclidean distance; group average link) (Clarke & Warwick 2001).

Spatial and temporal variations in the structure of fish assemblages were assessed by a two-way crossed analysis of similarities (ANOSIM, 9999 permutations), using matrices based on the Bray-Curtis similarity coefficient generated from abundance data (fourth-root transformed). Exploration of species contributions to typifying habitat types was carried out with the similarity of percentages SIMPER procedure. The abundance and biomass of these last species, and total fish abundance and biomass, were analysed by a factorial design with habitat and season as fixed factors through the distance-based *pseudo-F* statistics, PERMANOVA (9999 permutations, using unrestricted permutation of raw data). Although the study focused mostly on the differences among habitat types, the factor season was included nevertheless in the analysis. The interaction between the two factors was tested first, and, if interactions exist then comparisons among habitats were performed for each season, and those between seasons were carried out for each habitat. In case of no significant interactions, we considered the main effects of the two factors overall (Underwood 1997).

Cumulative dominance (*k*-dominance) curves were used to compare fish diversity among habitat types.

Statistical analyses were performed using the PRIMER software (Version 6.1.7).

Results

Habitat classification

Figure 2 presents the results of the MDS and cluster analyses and the classification of sampling sites into different habitat types. The first axis (MDS1) was highly negatively correlated with submerged vegetation density ($\rho = -0.94$) and cover ($\rho = -0.87$), reflecting that MDS1 clearly separated between sampling sites with unvegetated bottoms on the right part of the diagram and well-vegetated bottoms on the left. Additionally, MDS1 was negatively correlated with substrate particle heterogeneity ($\rho = -0.78$) and positively correlated with water depth ($\rho = 0.74$) and

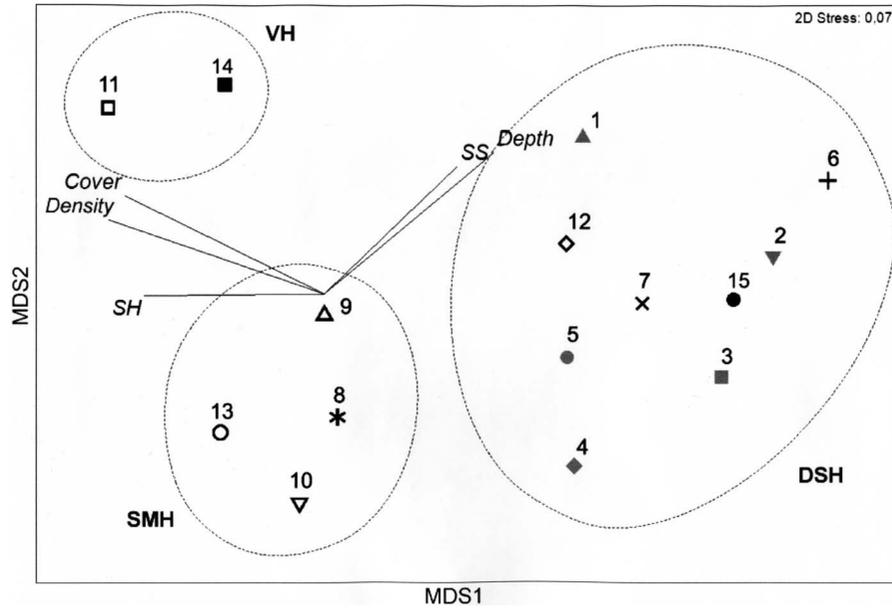


Figure 2. Ordination and classification of sampling sites into different habitat types according to the results of MDS and cluster analyses performed on the environmental variables matrix (DSH: deep sandy habitats; VH: vegetated habitats; SMH: shallow muddy habitats). Vectors represent the Pearson's correlation values between each environmental variable and the ordination scores (Cover: submerged vegetation cover; Density: submerged vegetation density; Depth: water depth; SS: substrate particle size; SH: substrate particle heterogeneity). Dashed lines represent clusters based on Euclidean distances of less than 3.

substrate particle size ($\rho = 0.58$). MDS2 was positively correlated with water depth ($\rho = 0.61$) and substrate particle size (0.55).

Therefore, sampling sites S1, S2, S3, S4, S5, S6, S7, S12 and S14, located on the right part of the diagram, showed low values of submerged vegetation cover and density, higher substrate particle size (sandy bottoms) and water depth (Figure 2 and Table I). Conversely, sampling sites S11 and S15 were represented by well-vegetated bottoms

(mean submerged vegetation cover higher than 35% and mean submerged vegetation density higher than 2) and higher substrate particle heterogeneity (Figure 2 and Table I).

Sampling sites S8, S9, S10 and S13, located in the lower part of the diagram, displayed muddy bottoms and relatively high values of submerged vegetation cover and density (Figure 2 and Table I).

According to these results, three differentiated littoral habitat types were defined: deep sandy

Table I. Mean annual values ± 1 SE of the environmental variables at each sampling site. Randomly selected sampling sites for the analysis of spatial and temporal patterns of fish community among habitat types: deep sandy habitats (DSH); vegetated habitats (VH); shallow muddy habitats (SMH), are shown in parenthesis.

Sampling site	Depth (cm)	Submerged vegetation cover (%)	Submerged vegetation density	Substrate particle size	Substrate particle heterogeneity
S1 La Chanta	51.9 \pm 4.6	25.6 \pm 9.4	1.2 \pm 0.5	2.10 \pm 0.01	0.35 \pm 0.02
S2 Tomás Maestre	57.1 \pm 6.0	7.9 \pm 6.4	0.5 \pm 0.4	2.18 \pm 0.07	0.43 \pm 0.09
S3 Los Aliseos ^(DSH)	46.5 \pm 5.6	5.8 \pm 4.8	0.4 \pm 0.3	2.17 \pm 0.07	0.47 \pm 0.09
S4 El Vivero	35.4 \pm 5.2	11.9 \pm 8.1	0.6 \pm 0.4	2.13 \pm 0.06	0.61 \pm 0.07
S5 Playa Arsenal	45.0 \pm 5.7	12.2 \pm 1.9	0.8 \pm 0.1	2.06 \pm 0.15	0.63 \pm 0.08
S6 Las Lomas ^(DSH)	63.0 \pm 5.2	6.7 \pm 6.7	0.5 \pm 0.5	2.25 \pm 0.11	0.53 \pm 0.08
S7 Los Nietos	52.9 \pm 4.3	12.3 \pm 8.1	0.6 \pm 0.4	2.02 \pm 0.07	0.53 \pm 0.05
S8 Lo Poyo ^(SMH)	38.3 \pm 1.5	21.5 \pm 7.2	1.3 \pm 0.4	1.70 \pm 0.08	0.63 \pm 0.02
S9 Punta Brava	39.7 \pm 5.5	30.4 \pm 7.3	1.5 \pm 0.4	1.83 \pm 0.06	0.53 \pm 0.05
S10 El Carmoli ^(SMH)	30.4 \pm 4.7	15.0 \pm 10.2	1.3 \pm 0.8	1.78 \pm 0.12	0.73 \pm 0.05
S11 Cartagonovo ^(VH)	41.7 \pm 2.1	36.9 \pm 14.4	2.1 \pm 0.7	2.10 \pm 0.18	0.90 \pm 0.13
S12 Los Alcázares	54.0 \pm 6.5	19.4 \pm 10.8	0.9 \pm 0.5	1.94 \pm 0.13	0.48 \pm 0.09
S13 La Hita ^(SMH)	35.3 \pm 3.0	28.1 \pm 11.4	1.4 \pm 0.5	1.61 \pm 0.12	0.63 \pm 0.07
S14 Lo Pagán ^(DSH)	51.9 \pm 5.2	9.0 \pm 7.3	0.7 \pm 0.4	2.01 \pm 0.02	0.31 \pm 0.04
S15 San Pedro ^(VH)	45.3 \pm 6.8	38.3 \pm 8.5	2.0 \pm 0.4	2.12 \pm 0.03	0.74 \pm 0.06

habitats (DSH), unvegetated bottoms composed predominantly of sand and gravel, vegetated habitats (VH) with well-developed meadows of the seagrass *C. nodosa* and substrate composed mainly of sand with the presence of large substrate types (mainly pebbles and boulders), shallow muddy habitats (SMH), shallow littoral areas with soft sediments (mainly mud) and small patches of submerged vegetation (*R. Cirrhosa* meadows and filamentous algae) (Table I).

The spatial and temporal analyses of fish assemblages were performed at eight sampling sites: DSH, sampling sites S3, S6 and S14; VH, sampling sites S11 and S15; SMH, sampling sites S8, S10 and S13 (Table I). Sites at DSH and SMH were randomly selected.

Fish community composition and structure

A total of 45,539 individuals were collected, representing 36 species from 18 fish families (Table II). The seven most abundant families were Mugilidae (50.2% of the total catches, five species), Gobiidae (26.5% of the total catches, four species), Atherinidae (9.5% of the total catches, one species), Sparidae (9.0% of the total catches, four species), Syngnathidae (2.1% of the total catches, three species), Blenniidae (1.5% of the total catches, two species) and Cyprinodontidae (1.0% of the total catches, one species).

The most frequent and abundant species in shallow littoral habitats were the mugilids *Liza saliens* and *L. aurata*, the marbled goby *Pomatoschistus marmoratus* and the sand smelt *A. boyeri* (Table II).

Overall fish abundance and biomass were higher in the shallow muddy habitats (SMH) (Table II). *S. aurata*, *L. ramada* and *Aphanius iberus* were much more abundant in SMH than in the other littoral habitats. Moreover, Soleidae species were caught exclusively in this habitat type (Table II).

A. boyeri, *Syngnathus abaster* and *Salaria pavo* were more abundant in VH (Table II). Sparidae species *Diplodus puntazzo*, *D. sargus* and *Sarpa salpa*, although less abundant than the previous three species, were much more abundant in VH (Table II).

The resident species *P. marmoratus* clearly dominated fish assemblages in DSH, although *L. aurata* and *L. saliens* were also abundant in this habitat (Table II).

The overall number of species was similar for the three littoral habitat types (Table II); however, cumulative dominance curves indicated that fish diversity was higher in VH and lower in DSH (Figure 3).

Comparisons among habitat types revealed that community structure varied widely (ANOSIM, Global R statistic = 0.199, $P < 0.001$). Pair-wise comparisons between habitat types showed significant differences for all combinations (ANOSIM_{DSH-VH}, R statistic = 0.188, $P < 0.001$; ANOSIM_{DSH-SMH}, R statistic = 0.267, $P < 0.001$; ANOSIM_{SMH-VH}, R statistic = 0.133, $P < 0.01$), indicating that the fish assemblage associated with DSH differed more than those of the other two habitats.

On the other hand, ANOSIM revealed a significant seasonal effect on fish community structure (ANOSIM, Global R statistic = 0.435, $P < 0.001$), with significant dissimilarities between all pair-wise comparisons (Table III). The greatest differences were encountered between summer and winter, and between summer and spring (Table III).

The SIMPER analysis showed that the mean assemblage similarity within the DSH was 55.52%, 53.16% for VH and 59.67% for SMH. The similarity of species contribution within these last two habitats was partitioned among more species than in DSH, since a total of 8 and 9 species were necessary to accumulate 90% of similarity in the first two habitats, while only 5 species were needed to reach such value in the later (Table IV). The species that most contributed to similarities within habitats were common among all three: *A. boyeri*, *L. saliens*, *L. aurata*, *P. marmoratus* and *S. aurata*, but with differences in their relative contribution within each habitat type. Other species with a high contribution in VH were *S. abaster* (11.63%), *S. pavo* (8.40%) and *A. iberus* (2.53%), whereas *S. abaster* (8.15%), *L. ramada* (4.10%), *M. cephalus* (3.56%) and *A. iberus* (3.43%) were the highest contributors in SMH.

Fish abundance and biomass

Interactions between habitat type and season were significant for *S. aurata* abundance and biomass, *A. iberus* abundance and biomass, *M. cephalus* biomass and *P. marmoratus* biomass (Table V). Thus, differences among habitats during each season and among seasons for each habitat type were examined in detail for these species.

In summer, there were only significant differences in *A. iberus* abundance and biomass among habitats, with significantly higher values in SMH as compared to VH ($P < 0.05$ for both comparisons) and DSH ($P < 0.05$ for both comparisons) (Table VI).

During autumn, *M. cephalus* biomass and *A. iberus* abundance were significantly lower in DSH with respect to SMH ($P < 0.05$) and VH ($P < 0.05$), respectively (Table VI).

Table II. Mean annual abundance (n. individuals/100 m²) and mean annual biomass (g individuals/100 m²) of the species caught in each habitat type (DSH, deep sandy habitats; VH, vegetated habitats; SMH, shallow muddy habitats). Habitat use: MM, marine migrants; R, resident species; MA, marine adventitious visitors.

Family	Species	Habitat use	DSH		VH		SMH	
			Abundance	Biomass	Abundance	Biomass	Abundance	Biomass
Anguillidae	<i>Anguilla anguilla</i>	MM	0.01	0.17	0.01	0.01	0	0
Atherinidae	<i>Atherina boyeri</i>	R	10.01	6.01	36.54	14.19	14.36	7.78
Blenniidae	<i>Lipophrys dalmatinus</i>	R	0.06	0.03	0.21	0.06	0	0
	<i>Salaria pavo</i>	R	1.39	1.41	4.94	4.16	3.18	2.48
Callionymidae	<i>Callionymus pusillus</i>	R	0.01	0.01	0.08	0.06	0	0
Carangidae	<i>Trachinotus ovatus</i>	MA	0	0	0.01	0.01	0	0
Clupeidae	<i>Sardina pilchardus</i>	MM	0.01	0.01	0	0	0	0
	<i>Sardinella aurita</i>	MM	0	0	0	0	0.01	0.03
Cyprinodontidae	<i>Aphanius iberus</i>	R	0.39	0.07	2.18	0.43	3.75	0.92
Engraulidae	<i>Engraulis encrasicolus</i>	MM	0.31	0.09	0	0	0	0
Gobiidae	<i>Pomatoschistus marmoratus</i>	R	64.46	21.43	39.24	12.80	61.94	24.31
	<i>Gobius cobitis</i>	R	0.41	1.03	0.73	1.61	1.33	0.08
	<i>Gobius paganellus</i>	R	0	0	0.26	0.30	0	0
	<i>Gobius niger</i>	R	0.24	0.60	0.48	1.23	1.21	6.91
Labridae	<i>Symphodus cinereus</i>	R	0.25	1.06	0.19	1.38	0.13	0.71
	<i>Symphodus ocellatus</i>	R	0.01	0.01	0	0	0	0
Moronidae	<i>Dicentrarchus labrax</i>	MM	0	0	0.06	0.01	0	0
	<i>Dicentrarchus punctatus</i>	MM	0	0	0.06	0.08	0	0
Mugilidae	<i>Liza aurata</i>	MM	36.20	19.61	41.81	21.90	62.97	37.61
	<i>Liza saliens</i>	MM	17.11	11.38	30.65	12.88	131.64	52.88
	<i>Liza ramada</i>	MM	0.11	0.01	0.14	0.08	14.52	3.34
	<i>Chelon labrosus</i>	MM	0	0	0.10	0.09	0	0
	<i>Mugil cephalus</i>	MM	0.01	0.01	0.18	0.03	2.00	1.08
Mullidae	<i>Mullus barbatus</i>	MM	0.01	0.12	0	0	0.02	0.02
Pomatomidae	<i>Pomatomus saltatrix</i>	MA	0	0	0	0	0.05	0.09
Poeciliidae	<i>Gambusia holbrooki</i>	R	0	0	0	0	0.01	0.03
Soleidae	<i>Pegusa impar</i>	R	0	0	0	0	0.02	0.10
	<i>Solea senegalensis</i>	MM	0	0	0	0	0.02	0.04
	<i>Solea solea</i>	MM	0	0	0	0	0.14	0.20
Sparidae	<i>Diplodus puntazzo</i>	MM	0.96	0.34	1.38	1.25	0.71	0.38
	<i>Diplodus sargus</i>	MM	0.08	0.01	1.07	0.07	0	0
	<i>Sparus aurata</i>	MM	4.35	1.33	13.58	2.54	36.50	6.24
	<i>Sarpa salpa</i>	MM	0.38	0.38	1.35	1.62	0	0
Syngnathidae	<i>Hippocampus guttulatus</i>	R	0.03	0.01	0.01	0.03	0.01	0.01
	<i>Syngnathus abaster</i>	R	0.48	0.29	9.39	2.46	3.36	1.23
	<i>Syngnathus typhle</i>	R	0.01	0.11	0.10	0.14	0.03	0.03
Total			138.05	65.76	184.74	79.38	338.06	146.49
Species richness			25		26		23	

During winter, there were significant differences in the abundance and biomass of *S. aurata*, which showed the lowest values in DSH ($P < 0.05$ for all pair-wise comparisons). *M. cephalus* biomass was significantly higher in SMH in regard to the other two habitats ($P < 0.05$ for both pair-wise comparisons), and *P. marmoratus* biomass was lowest in VH compared to DSH and SMH ($P < 0.01$ for both pair-wise comparisons) (Table VI).

In spring, habitat effect was significant for *M. cephalus* biomass, which was the highest in SMH ($P < 0.001$ for both pair-wise comparisons) (Table VI).

With regard to seasonal variation, *S. aurata* abundance and biomass displayed significant

seasonal fluctuations in the three habitat types with significantly higher values during winter and spring ($P < 0.05$ for all pair-wise comparisons) (Table VI).

A. iberus showed significant seasonal differences in VH and SMH. Pair-wise tests revealed that in VH abundance was lower during winter in regard to autumn ($P < 0.05$) and, in SMH, summer abundance and biomass were significantly higher than winter and spring ($P < 0.01$ for all pair-wise comparisons) (Table VI).

Finally, *P. marmoratus* biomass in VH was significantly lower during summer compared to autumn ($P < 0.05$) and spring ($P < 0.05$), and in SMH it was the lowest during summer ($P < 0.05$ for

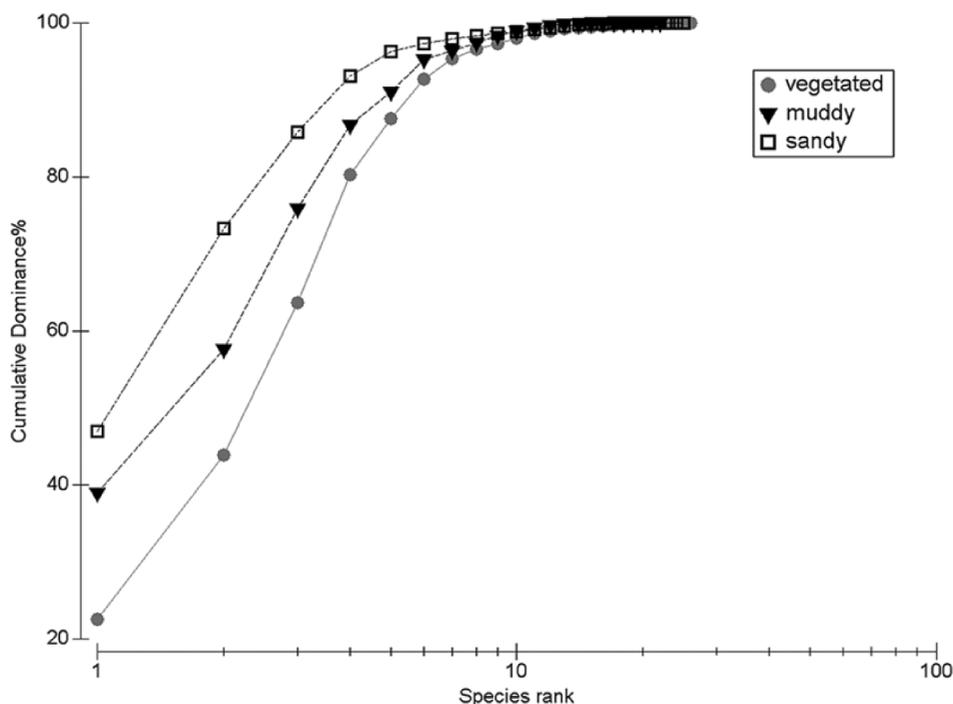


Figure 3. Cumulative ranked abundances of fish plotted against species rank as depicted by k -dominance curves to examine differences in fish diversity among habitat types.

Table III. R statistic values (bold) and their significance levels (P) for pair-wise comparisons of fish community structure, based on fish abundance data, using ANOSIM for differences among seasons.

	Summer	Autumn	Winter	Spring
Summer		0.258	0.735	0.595
Autumn	0.001		0.508	0.384
Winter	0.001	0.001		0.177
Spring	0.001	0.001	0.001	

all pair-wise comparisons). In DSH, *P. marmoratus* biomass was higher during winter in regard to summer ($P < 0.001$) and autumn ($P < 0.05$) (Table VI).

A. boyeri showed a significant seasonal difference in its abundance (Table V), with significantly higher values during summer, followed by autumn and spring, whereas the lowest values were detected during winter ($P < 0.05$ for all pair-wise comparisons) (Table VI).

M. cephalus abundance was significantly higher in SMH in regard to the other two habitats ($P < 0.05$ for both pair-wise comparisons) (Tables V and VI).

There were only significant differences among habitats in the abundance and biomass of *L. saliens* and *L. ramada* (Table V), with the highest values found in SMH for both species (*L. saliens*:

$P < 0.01$ for all pair-wise comparisons; *L. ramada*: $P < 0.05$, for all pair-wise comparisons) (Table VI).

L. aurata only presented a highly significant variation in abundance and biomass among seasons (Table V). Pair-wise tests showed that abundance and biomass were significantly higher during winter and spring ($P < 0.001$ for all pair-wise comparisons) (Table VI).

The significant seasonal differences in the abundance and biomass of *S. pavo* (Table V) were due to higher values obtained in the summer ($P < 0.001$ for all pair-wise comparisons) (Table VI).

The abundance and biomass of *S. abaster* varied significantly among habitats, whereas its distribution was homogeneous among seasons (Table V). Considering habitat differences, abundance and biomass were significantly higher in VH, followed by SMH, whereas the lowest values were detected in DSH ($P < 0.05$ for all pair-wise comparisons) (Table VI).

Total fish abundance and biomass presented a significant variation among habitats, whereas seasonal variation was only significant for total fish biomass (Table V). Taking into account habitat differences, total fish abundance was the lowest in DSH ($P < 0.05$) and total fish biomass was significantly higher in SMH compared to DSH ($P < 0.01$). Seasonal differences were due to higher values of total fish biomass obtained in spring compared to

Table IV. Results of SIMPER analysis with species contributions to similarities within habitat types. Avg Sim: average similarity; Sim/SD: ratio of AVG Sim to standar deviation; Contrib%: the percentage each species contributes to similarities; Cum%: cumulative percent of total similarity; Avg abund: average abundance by shoreline type (is based on values in the Bray-Curtis similarity matrix and does not represent true abundance estimates).

Species	Avg Abund	Avg Sim	Sim/SD	Contrib%	Cum%
Vegetated habitats (VH)					
<i>Atherina boyeri</i>	1.83	9.90	1.26	18.62	18.62
<i>Liza saliens</i>	1.93	8.27	1.03	15.55	34.18
<i>Pomatoschistus marmoratus</i>	2.05	7.90	0.98	14.86	49.04
<i>Syngnathus abaster</i>	1.39	6.18	1.02	11.63	60.67
<i>Liza aurata</i>	1.60	5.18	0.67	9.74	70.41
<i>Sparus aurata</i>	0.92	5.16	0.56	9.71	80.12
<i>Salaria pavo</i>	0.79	4.47	0.76	8.40	88.52
<i>Aphanius iberus</i>	0.58	1.35	0.40	2.53	91.05
Shallow muddy habitats (SMH)					
<i>Pomatoschistus marmoratus</i>	2.54	13.1	1.59	21.96	21.96
<i>Liza saliens</i>	2.95	12.98	1.57	21.75	43.71
<i>Atherina boyeri</i>	1.57	6.23	1.16	10.44	54.15
<i>Liza aurata</i>	1.76	6.02	0.97	10.09	64.24
<i>Sparus aurata</i>	1.22	5.63	0.77	9.44	73.68
<i>Syngnathus abaster</i>	1.17	4.86	1.09	8.15	81.83
<i>Liza ramada</i>	0.88	2.44	0.62	4.1	85.92
<i>Mugil cephalus</i>	0.7	2.12	0.66	3.56	89.48
<i>Aphanius iberus</i>	0.68	2.05	0.41	3.43	92.91
Deep sandy habitats (DSH)					
<i>Pomatoschistus marmoratus</i>	2.77	21.91	2.33	39.46	39.46
<i>Liza aurata</i>	1.72	11.41	1.08	20.55	60.01
<i>Atherina boyeri</i>	1.29	8.55	0.92	15.4	75.41
<i>Liza saliens</i>	1.28	5.02	0.67	9.04	84.44
<i>Sparus aurata</i>	0.66	3.29	0.53	5.92	90.37

Table V. *Pseudo-F* values and significance levels for the PERMANOVAs of abundance and biomass of the main species typifying habitat types, according SIMPER analysis, and total fish abundance and biomass, with habitat type (H) and season (S) as fixed factors. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; (ns) not significant.

Species	Abundance			Biomass		
	H	S	H x S	H	S	H x S
<i>Aphanius iberus</i>	6.40**	7.26***	3.58**	7.06**	4.61**	3.80**
<i>Atherina boyeri</i>	1.67 _(ns)	4.16**	1.45 _(ns)	0.37 _(ns)	1.99 _(ns)	1.50 _(ns)
<i>Liza aurata</i>	0.91 _(ns)	8.50***	0.68 _(ns)	0.91 _(ns)	6.98***	1.09 _(ns)
<i>Liza ramada</i>	4.10**	2.16 _(ns)	1.96 _(ns)	3.49**	1.33 _(ns)	1.29 _(ns)
<i>Liza saliens</i>	7.83***	0.89 _(ns)	0.81 _(ns)	8.77***	1.53 _(ns)	0.60 _(ns)
<i>Mugil cephalus</i>	5.98***	1.57 _(ns)	1.31 _(ns)	2.96**	1.78 _(ns)	1.77*
<i>Pomatoschistus marmoratus</i>	1.64 _(ns)	2.46 _(ns)	1.38 _(ns)	2.40 _(ns)	7.19**	2.23*
<i>Salaria pavo</i>	0.92 _(ns)	8.86***	0.89 _(ns)	1.45 _(ns)	6.26**	1.56 _(ns)
<i>Sparus aurata</i>	3.53*	9.85***	3.89**	4.28**	8.89***	3.14**
<i>Syngnathus abaster</i>	10.67***	2.02 _(ns)	2.10 _(ns)	11.08***	2.15 _(ns)	1.99 _(ns)
Total	5.07**	1.07 _(ns)	1.06 _(ns)	4.51**	4.29**	1.21 _(ns)

summer ($P < 0.001$) and autumn ($P < 0.01$), and higher values during winter in regard to summer ($P < 0.01$) (Table VI).

Discussion

The results show that the predominant families were Mugilidae, Gobiidae, Sparidae and Atherinidae, which corresponds to findings made in other

European coastal lagoons (Gordo & Cabral 2001; Koutrakis et al. 2005; Pombo et al. 2005; Franco et al. 2006; Ribeiro et al. 2006; Maci & Basset, 2009). Species belonging to the families Mugilidae (size range: 12–148 mm), Sparidae (size range: 14–72 mm) and Atherinidae (size range: 9–86 mm), mainly use these areas during their juvenile stages (Verdiell-Cubedo et al. 2006). Since many of these species are important for the local fishing industry,

Table VI. Seasonal variation of abundance (n. individuals/100 m²) and biomass (g individuals/100 m²) of the main species typifying habitat types, according SIMPER analysis, and total fish abundance (n. individuals/100 m²) and total fish biomass (g individuals/100 m²), in each habitat type (mean value \pm 1 SE).

Species	Summer		Autumn		Winter		Spring	
	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass
Sandy habitat								
<i>Aphanius iberus</i>	1.35 \pm 0.88	0.23 \pm 0.15	0.21 \pm 0.15	0.04 \pm 0.02	0	0	0.04 \pm 0.04	0.03 \pm 0.03
<i>Atherina boyeri</i>	23.49 \pm 9.25	10.31 \pm 4.90	13.13 \pm 3.68	15.75 \pm 5.99	0.37 \pm 0.22	0.11 \pm 0.08	2.08 \pm 0.57	1.45 \pm 0.42
<i>Liza aurata</i>	0.21 \pm 0.12	0.68 \pm 0.40	5.42 \pm 3.97	0.80 \pm 0.56	74.48 \pm 29.28	39.59 \pm 13.23	38.96 \pm 9.19	28.57 \pm 6.18
<i>Liza ramada</i>	0	0	0	0	0.31 \pm 0.31	0.03 \pm 0.03	0.08 \pm 0.08	0.02 \pm 0.02
<i>Liza saliens</i>	4.90 \pm 2.13	1.36 \pm 0.58	29.86 \pm 17.26	6.59 \pm 3.11	21.04 \pm 14.67	10.11 \pm 6.58	16.08 \pm 6.60	17.27 \pm 10.07
<i>Mugil cephalus</i>	0	0	0.07 \pm 0.07	0.04 \pm 0.04	0	0	0	0
<i>Pomatoschistus marmoratus</i>	75.10 \pm 29.30	6.49 \pm 2.54	68.06 \pm 27.72	16.12 \pm 5.91	70.68 \pm 12.09	28.41 \pm 6.29	46.54 \pm 16.43	23.08 \pm 7.41
<i>Salaria pavo</i>	4.64 \pm 2.91	2.32 \pm 1.25	0.21 \pm 0.21	0.17 \pm 0.17	0	0	0.63 \pm 0.24	2.16 \pm 1.05
<i>Sparus aurata</i>	0	0	0	0	7.60 \pm 3.71	0.82 \pm 0.40	7.83 \pm 3.03	3.60 \pm 1.29
<i>Syngnathus abaster</i>	0	0	0.35 \pm 0.15	0.06 \pm 0.02	0.63 \pm 0.48	0.69 \pm 0.59	0.83 \pm 0.30	0.35 \pm 0.12
Total	114.22 \pm 30.80	24.91 \pm 5.61	120.22 \pm 48.54	47.20 \pm 13.56	196.30 \pm 25.82	91.36 \pm 12.53	118.64 \pm 22.47	81.70 \pm 14.69
Vegetated habitat								
<i>Aphanius iberus</i>	2.77 \pm 1.62	0.30 \pm 0.22	2.73 \pm 1.30	0.87 \pm 0.43	0.23 \pm 0.17	0.09 \pm 0.06	1.95 \pm 1.70	0.55 \pm 0.48
<i>Atherina boyeri</i>	87.50 \pm 43.43	38.10 \pm 22.46	12.56 \pm 3.73	2.47 \pm 0.88	1.14 \pm 0.56	0.31 \pm 0.17	9.69 \pm 6.06	4.45 \pm 2.57
<i>Liza aurata</i>	0.09 \pm 0.06	0.14 \pm 0.13	16.25 \pm 6.29	1.95 \pm 0.85	46.48 \pm 26.17	30.98 \pm 18.11	92.50 \pm 23.21	67.82 \pm 18.33
<i>Liza ramada</i>	0.05 \pm 0.05	0.22 \pm 0.22	0	0	0.46 \pm 0.21	0.05 \pm 0.02	0.08 \pm 0.08	0.02 \pm 0.02
<i>Liza saliens</i>	16.56 \pm 7.05	14.26 \pm 6.16	41.36 \pm 20.58	10.68 \pm 5.24	20.85 \pm 9.77	7.50 \pm 3.27	22.73 \pm 13.83	15.46 \pm 6.34
<i>Mugil cephalus</i>	0.04 \pm 0.04	0.01 \pm 0.01	0.68 \pm 0.45	0.10 \pm 0.06	0	0	0	0
<i>Pomatoschistus marmoratus</i>	22.19 \pm 11.84	6.44 \pm 2.50	67.27 \pm 21.50	18.08 \pm 6.39	15.80 \pm 6.81	9.58 \pm 4.02	31.09 \pm 6.89	17.08 \pm 3.62
<i>Salaria pavo</i>	15.13 \pm 7.01	8.34 \pm 3.55	0.28 \pm 0.10	0.31 \pm 0.17	0.06 \pm 0.06	0.16 \pm 0.16	0.94 \pm 0.39	2.53 \pm 1.27
<i>Sparus aurata</i>	0	0	0	0	20.45 \pm 7.47	4.95 \pm 2.33	18.05 \pm 9.29	5.39 \pm 2.47
<i>Syngnathus abaster</i>	12.10 \pm 5.05	3.43 \pm 1.23	7.78 \pm 3.60	1.58 \pm 0.76	1.65 \pm 0.58	0.55 \pm 0.20	8.13 \pm 3.38	2.78 \pm 0.89
Total	205.89 \pm 48.83	83.29 \pm 26.86	156.59 \pm 31.39	49.24 \pm 10.61	166.81 \pm 45.15	56.30 \pm 20.59	232.03 \pm 43.85	146.91 \pm 20.55

(Continued)

Table VI. (Continued).

Species	Summer		Autumn		Winter		Spring	
	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass
<i>Aphanius iberus</i>	12.89 ± 5.34	2.92 ± 1.30	3.31 ± 1.85	0.82 ± 0.44	1.00 ± 1.00	0.32 ± 0.32	0.38 ± 0.21	0.21 ± 0.16
<i>Atherina boyeri</i>	26.02 ± 11.27	7.69 ± 4.03	16.56 ± 11.77	9.05 ± 5.59	3.44 ± 2.15	1.02 ± 0.42	9.31 ± 4.15	3.63 ± 1.39
<i>Liza aurata</i>	0.16 ± 0.16	0.55 ± 0.55	5.13 ± 1.93	0.74 ± 0.27	70.56 ± 41.11	27.16 ± 12.31	151.88 ± 86.32	122.10 ± 76.66
<i>Liza ramada</i>	0	0	0.06 ± 0.06	0.79 ± 0.79	7.13 ± 3.47	2.61 ± 1.97	17.13 ± 9.94	2.11 ± 0.88
<i>Liza saltans</i>	69.77 ± 17.20	17.19 ± 5.11	115.44 ± 42.52	45.23 ± 15.78	148.19 ± 138.03	33.97 ± 21.07	68.75 ± 29.79	76.35 ± 43.28
<i>Mugil cephalus</i>	0	0	1.50 ± 0.43	0.36 ± 0.18	1.25 ± 0.81	0.44 ± 0.32	1.31 ± 0.46	3.53 ± 2.76
<i>Pomatoschistus marmoratus</i>	14.06 ± 7.93	2.30 ± 1.18	60.56 ± 33.47	29.61 ± 11.88	88.50 ± 20.92	46.18 ± 9.96	30.63 ± 9.54	12.85 ± 2.99
<i>Salaria pavo</i>	12.34 ± 7.36	5.55 ± 2.31	0.56 ± 0.40	2.37 ± 1.60	0.25 ± 0.19	1.66 ± 1.46	0.31 ± 0.17	0.88 ± 0.47
<i>Sparus aurata</i>	0	0	0.25 ± 0.19	0.13 ± 0.11	133.31 ± 53.86	18.19 ± 7.11	9.31 ± 3.29	6.79 ± 3.11
<i>Syngnathus abaster</i>	2.58 ± 1.62	0.95 ± 0.63	4.56 ± 1.39	1.69 ± 0.58	1.88 ± 0.67	0.68 ± 0.24	3.81 ± 1.17	1.84 ± 0.58
Total	140.94 ± 24.84	43.67 ± 7.62	285.13 ± 50.89	123.33 ± 26.84	560.81 ± 221.92	134.21 ± 38.88	391.19 ± 154.85	288.49 ± 131.44

the shallow littoral areas of the lagoon gain a special importance for fisheries, since they act as a nursery or feeding grounds for marine migrant species and resident species which are of commercial interest. From a conservationist point of view, the presence of threatened species included in regional, national or international red lists must be noted. The shallow areas of the lagoon provide refuge and essential habitats for endangered species like *A. iberus*, *A. anguilla*, *Hippocampus guttulatus*, *S. abaster* and *P. marmoratus*, which confers an added value to the results of this study from the conservation perspective.

Despite the ubiquitous character of some of the most abundant species (*A. boyeri*, *L. saliens*, *L. aurata*, *P. marmoratus* and *S. aurata*) and the low abundances of typical seagrass species like *S. typhle* and *H. guttulatus*, the results revealed the presence of significant differences in fish community structure according to the habitat types distinguished in this study.

It is worth pointing out the low number of species closely associated with seagrasses found in the Mar Menor compared to other European coastal lagoons. For example, in Venice and Ria Formosa lagoons, researchers have reported a significantly high number of species belonging to the Syngnathidae family (*Syngnathus acus*, *S. taenionotus*, *S. tenuirostris*, *Nerophis ophidion*, *N. lumbriciformes*) or the presence of specialised gobies like *Zosterisessor ophiocephalus* (Franco et al. 2006; Ribeiro et al. 2006). This situation could be attributed to geographical variation in the composition of the regional fish species pool, or to the fact that historically, the Mar Menor has displayed scarce development of seagrass meadows due to its hypersaline environmental conditions (up to 70 at the end of the 18th century) (Pérez-Ruzafa et al. 2005).

The fish assemblage that differed most from the others was DSH. Probably, this was due to greater structural complexity and food availability in VH and SMH habitat types, which possibly increased their capacity to maintain a more diverse and abundant fish community. Habitat complexity is one of the main environmental factors influencing fish assemblages in estuaries and coastal lagoons because complex habitats possess favourable conditions that provide abundant food resources and refuge against predators for the different stages of fish species (Franco et al. 2006; Ribeiro et al. 2006; França et al. 2009).

SMH are the shallowest littoral areas and have a soft substrate (mainly composed of mud) with small patches of submerged vegetation, the phanerogams *C. nodosa* and *R. cirrhosa* and filamentous algae of the genera *Cladophora* and *Chaetomorpha*. These

habitats, adjacent to the perimetral lagoon marshlands, displayed a total abundance and biomass higher than the other habitat types (as much as three times greater than that of the DSH). The highest captures of juveniles of migrant fish species such as *L. saliens*, *L. ramada*, *M. cephalus* and *S. aurata*, and the resident species *P. marmoratus*, characterised these sites. It has been demonstrated that marshlands provide abundant food resources for the earlier life stages of the migrant fish species (França et al. 2011). This situation, combined with lower water depth that offer better protection against predators (França et al. 2009), may play an important role in determining the suitability of this habitat to the aforementioned fish species. On the other hand, it has also been observed that the sand goby *P. marmoratus* is abundant and frequently the dominant species in habitats characterised by muddy and sandy bottoms with scarce submerged vegetation development (Koutrakis et al. 2005; Franco et al. 2006), an observation supported by the results of the present study.

Similarly, high abundance and biomass values were obtained for *A. iberus*, mainly in summer, when these littoral areas feature high cover and density of submerged vegetation as a result of development of small patches of *R. cirrhosa* and filamentous algae, which favours the presence of *A. iberus* (Alcaraz et al. 2008; Oliva-Paterna et al. 2009). For this reason, these littoral habitats, together with the adjacent marshlands of Lo Poyo, El Carmolí and La Hita, constitute important areas for the conservation of natural populations of this endangered species in the Mar Menor and, to a certain extent, in its geographical distribution range.

VH are characterised by heterogeneous substrate composed predominantly of fine sediments (from mud to sand) with presence of pebbles and boulders. These bottoms also support well-developed meadows, in terms of cover and density, of either the phanerogam *C. nodosa* or a mixture of *C. nodosa* and the alga *C. prolifera*. VH distinguished by their high abundance of *S. abaster*, *S. aurata*, *A. boyeri* and *S. pavo*. The former species showed the greatest abundance in the VH, as this species displays morphological and behavioural adaptations that permit it to develop its life cycle on the leaves of aquatic phanerogams (Malavasi et al. 2007).

It was also observed that VH habitats act as important recruitment areas for juveniles of migrant fish species. These bottoms are characterised by abundant *S. aurata* and *L. saliens* juveniles, which coincides with the results obtained by França et al. (2009) in estuarine systems along the Portuguese coast and by Franco et al. (2006) in Venice lagoon, and suggest that this habitat might play an important

role as a suitable nursery area for several commercially important fish species. Similarly, two of the most abundant resident species, *A. boyeri* and *S. pavo*, showed high abundances in the VH. These findings are partly explained by the biology of these species. For example, *A. boyeri* reproduces in the lagoon during spring and early summer (Andreu-Soler et al. 2006), attaching its eggs to submerged vegetation (Fernández-Delgado et al. 2000), behaviour that is reflected in the substantially increased numbers of juveniles caught during summer in this habitat type. This seasonal pattern coincides with the results obtained by Maci & Basset (2010) in Acquatina lagoon (Italy) where abundance of small-sized individuals of *A. boyeri* were higher during summer. On the other hand, Verdiell-Cubedo et al. (2008) demonstrated that juvenile individuals of *S. pavo* were abundant in the seagrass meadows of the Mar Menor. The great structural complexity of the seagrass beds, their low hydrodynamism and the abundant presence of food resources in the form of invertebrates, epiphytes and detritus (Mistri et al. 2000; Almeida et al. 2008) are probably key factors that could increase the growth and survival of juvenile fishes in these habitats (Franco et al. 2006; Ribeiro et al. 2006).

VH and SMH are mainly found on the western shoreline of the lagoon, and are adjacent to the perimetral lagoon wetlands (Lo Poyo, El Carmolí, La Hita and San Pedro) or nearby shallow areas (Cartagonovo and Punta Brava) that are still near pristine. Moreover, these areas could enhance their productivity by the presence of seasonal watercourse mouths that carry large quantities of sediments, nutrients and terrestrial organic matter (Lloret et al. 2005; Velasco et al. 2006).

Finally, DSH are characterised by a homogeneous substrate formed mainly of sand and gravel, their relative higher depth and scarce development of submerged vegetation. This type of habitat mainly corresponds to sandy beaches (natural or not) of the perimetral urbanised areas of the lagoon. They presented lower fish diversity and their fish assemblages were dominated by the resident goby *P. marmoratus*, and the marine migrants *L. aurata* and *L. saliens*, findings that coincide with those of Franco et al. (2006), and Ribeiro et al. (2006). *P. marmoratus* has been described as a generalist species in terms of habitat preferences and it shows wide distribution in the Mar Menor (Verdiell-Cubedo et al. 2008).

In regards to temporal fish assemblage patterns, the mean total abundance and biomass were maximal during winter and spring, mainly due to high captures of juveniles from migrant species such *L. aurata*, *L. saliens*, *L. ramada* and *S. aurata*

whose recruitment occurs in the lagoon during these seasons. This finding differs from the results obtained in the coastal lagoons of Óbidos and Ria Formosa (Portugal) (Gordo & Cabral 2001; Ribeiro et al. 2006), Venice and Acquatina (Italy) (Franco et al. 2006; Maci & Basset 2009) and Porto-Lagos (Greece) (Koutrakis et al. 2005), where maximum abundance values were registered during warmer months. This temporal variability could be attributed to geographical differences in the environmental factors (water temperature, hydrodynamics, etc.) that regulate fish reproduction and inward migration periods of larvae and juvenile individuals (Martinho et al. 2009).

Conversely, higher abundance and biomass values for resident species (*A. boyeri*, *S. pavo*, *A. iberus* and *S. abaster*) were observed in summer, which suggest some temporal segregation between resident and migrant fish species in the shallow littoral areas of the lagoon.

In conclusion, this study emphasizes the importance of the shallow littoral areas of the Mar Menor to numerous fish species, including those of commercial and conservationist interest. Moreover, the results also highlight that fish community differed according to the different habitat types identified. These habitat-related differences were likely associated with changes in structural complexity among habitats, and suggest that maintenance and recovery of habitat heterogeneity within the littoral zone of coastal lagoons should be a priority in the management of coastal fisheries and some endangered fish species.

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