

Macroecological analysis of the fish fauna inhabiting *Cymodocea nodosa* seagrass meadows

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In this study, patterns in the taxonomic richness and composition of the fish fauna inhabiting *Cymodocea nodosa* seagrass meadows were described across their entire distribution range in the Mediterranean Sea and adjacent Atlantic Ocean. Specifically, the study tested whether there are differences in the composition of fish assemblages between those ecoregions encompassed by the distribution range of *C. nodosa*, and whether these differences in composition are connected with differences in bioclimatic affinities of the fish faunas. A literature review resulted in a total of 19 studies, containing 22 fish assemblages at 18 locations. The ichthyofauna associated with *C. nodosa* seagrass meadows comprises 59 families and 188 species. The western Mediterranean (WM) Sea has the highest species richness (87 species). Fish assemblages from the Macaronesia–Canary Islands, the Sahelian Upwelling, South European Atlantic Shelf and the WM differ, in terms of assemblage composition, relative to other ecoregions. In contrast, the composition of the fish fauna from the central and eastern Mediterranean overlaps. There is a significant serial correlation in fish assemblage composition between adjacent ecoregions along the distribution range of *C. nodosa*. Dissimilarities in assemblage composition are connected with the geographical separation between locations, and the mean minimum annual seawater temperature is the environmental factor that explains most variation in fish assemblage composition.

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INTRODUCTION

Understanding patterns in the composition and diversity of biological entities is a major goal of ecology (Briggs, 1974; Roy *et al.*, 1998; Spalding *et al.*, 2007). While coastal ecologists have mainly focused their efforts towards describing patterns of variation in the distribution, composition and abundance of biological assemblages at small and intermediate scales, *i.e.* from a few cm to hundreds of m (Fraschetti *et al.*, 2005), a wealth of studies have been conducted in the last decade to describe ecological patterns at broad scales (Tuya *et al.*, 2008; Hawkins *et al.*, 2009; Wernberg *et al.*, 2010,

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2011a, b). Without a doubt, these studies have contributed to a renewed interest in the field of marine macroecology, an interface discipline between ecology and biogeography, which may be defined as a non-experimental approach that aims to identify ecological patterns at scales much larger than those of traditional ecological studies (Brown, 1995). In a global change context, macroecological analyses describing large-scale patterns in the composition and structure of biological communities, and so inferring processes that create such patterns, have important implications in ecology, evolutionary biology and conservation (Briggs, 1974; Roy *et al.*, 1998). For example, understanding how latitudinal gradients in climatic variables influence the distribution and abundance of marine organisms can help out to ascertain future climatic scenarios in patterns of distribution and abundance of the marine biota (Hawkins *et al.*, 2009; Hofstede & Rijnsdorp, 2011; Merzouk & Johnson, 2011; Wernberg *et al.*, 2011a, b; Tuya *et al.*, 2012). These results may be particularly relevant for predicting the effects of climate change (Wernberg *et al.*, 2010); in turn, shifts in the distribution patterns of biota along latitudinal gradients have been one of the main detectable responses of both aquatic and terrestrial organisms to global warming (Walther *et al.*, 2002; Parmesan & Yohe, 2003; Poloczanska *et al.*, 2007; Wernberg *et al.*, 2011b).

Seagrasses provide a crucial nearshore habitat for numerous fish species, particularly during their early life stages, where small-sized fishes find food and shelter along these nursery grounds (Arrivillaga & Baltz, 1999; Duarte, 2000; Beck *et al.*, 2001; Espino *et al.*, 2011). Despite the fact that fish assemblages associated with seagrass meadows have been locally described all around the world in tropical, subtropical and temperate regions, descriptions of spatial variation of ecological attributes of fish assemblages from regional to biogeographical scales, *i.e.* larger than hundreds of km of separation, are comparatively scarce (Gillanders, 2006). Still, some relevant efforts in some parts of the world have been implemented (Weinstein & Heck, 1979; Worthington *et al.*, 1992; Ferrell *et al.*, 1993; Costa *et al.*, 2002; Wyda *et al.*, 2002).

The seagrass *Cymodocea nodosa* (Ucria) Ascherson is distributed across the entire Mediterranean Sea and the adjacent eastern Atlantic coasts, from southern Portugal to Senegal, including the oceanic archipelagos of Madeira and the Canaries (Barberá *et al.*, 2005). According to the seminal model of bioregionalization of coastal and shelf areas of the world (Spalding *et al.*, 2007), meadows constituted by the seagrass *C. nodosa* are found within three marine provinces (Lusitanian, Mediterranean Sea and West African Transition), encompassing 11 ecoregions in the northern hemisphere. Local descriptions of patterns in the diversity and abundance of fish assemblages have been accomplished across almost the entire distributional range of *C. nodosa* (except at the coasts of northern Africa, where there is a lack of specific works), particularly ascertaining associations between the physical structure of the seagrass habitat and their fish inhabitants. Nevertheless, a detailed macroecological analysis of patterns in the diversity and composition of the fish fauna is lacking. In this study, patterns in the richness and composition (*i.e.* presence of taxa) of the fish fauna inhabiting *C. nodosa* seagrass meadows across their entire distribution range were described, at the level of family and species. In particular, this study tests whether there are differences in the richness and composition of fish assemblages between ecoregions and whether these differences in composition are connected with differences in bioclimatic affinities of the fish faunas.

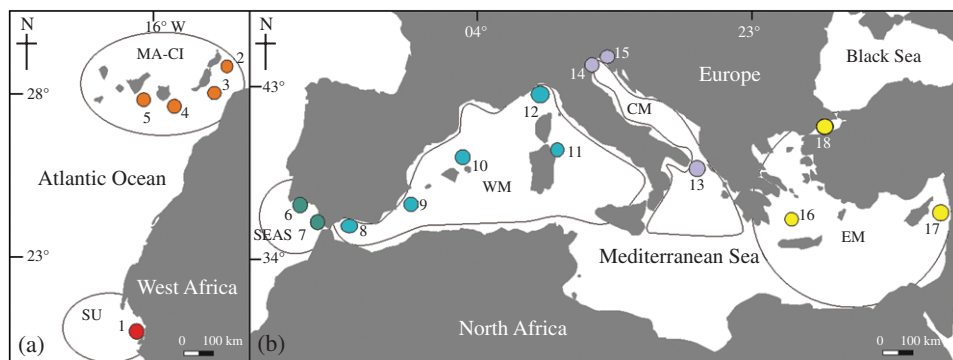


FIG. 1. Map showing the position of each sampling location at (a) the north-eastern Atlantic Ocean, including: Banc d'Arguin (1), Lanzarote Island (2), Fuerteventura Island (3), Gran Canaria Island (4) and Tenerife Island (5), and (b) the north-eastern Atlantic and Mediterranean Sea: Ria Formosa Lagoon (6), Cádiz Bay (7), Málaga Bay (8), Mar Menor (9), Menorca Island (10), Sardinia Island (11), Gulf of Imperia (12), Acquatina Lagoon (13), Venice Lagoon (14), Gulf of Trieste (15), Cyclades Islands (16), Lebanon (17) and Erdek Bay (18). For ecoregions, see Table I.

MATERIALS AND METHODS

DATA COMPILATION

A literature review, including unpublished reports (*i.e.* grey literature), on ichthyofauna associated with *C. nodosa* seagrass meadows was accomplished, resulting in a total of 19 studies (16 published in peer-reviewed journals and three unpublished reports), comprising 22 fish assemblages at 18 locations (Fig. 1 and Table I). For each location, fish data from monospecific *C. nodosa* meadows and meadows mixed with other vegetation at some locations were extracted (Table I). The works of Harmelin-Vivien *et al.* (2005), Maci & Basset (2009) and Giakoumi *et al.* (2012) did not provide data on fishes inhabiting in *C. nodosa* meadows. These authors, however, were personally consulted and provided data on fishes living in these particular *C. nodosa* beds. Presence–absence matrices, at the level of family and species, were then created (Table SI, Supporting Information). Since these studies were carried out at different times, all recorded fish species were revised and cited according to the online Catalogue of Fishes (Eschmeyer, 2015). The large variety of sampling methods may have affected the results of this work; different techniques may vary their efforts according to species' biological attributes, *e.g.* their ability to swim and escape from different types of fishing gear. This problem, however, is considerably reduced as the study exclusively focused on composition (presence or absence) data. Moreover, at some ecoregions, several complementary methods were implemented, limiting any bias towards determination of fish fauna composition in this sense. Locations were grouped within ecoregions according to the bioregionalization of coastal and shelf areas of the world (Spalding *et al.*, 2007), with some modifications due to the lack of data in some areas, in particular: the western Mediterranean (WM) and Alborán Seas were grouped within the WM; the Adriatic and Ionian Seas were grouped within the central Mediterranean (CM); finally, the Marmara, Aegean and Levantine Seas were grouped within the eastern Mediterranean (EM). As a result, six ecoregions were considered: Sahelian Upwelling (SU), Macaronesia–Canary Islands (MA-CI), South European Atlantic Shelf (SEAS), WM, CM and EM.

Fish species were arranged in seven bioclimatic categories according to their worldwide distribution (Froese & Pauly, 2014), and a previous categorization from the study region (Henriques *et al.*, 2007), including: (1) cold-temperate, species that have their southern limits at, or near, the Atlantic coast of the Iberian Peninsula and extend in range into the North Sea, or towards boreal latitudes; (2) Macaronesian, species exclusively occurring in the Macaronesian archipelagos; (3) Mediterranean, species that only occur in the temperate Mediterranean Sea; (4) temperate, species present in the whole temperate Lusitanian Province (*sensu* Almada *et al.*,

TABLE 1. Studies on fish assemblages associated with *Cymodocea nodosa* seagrass meadows, including authors, locations and numbers (see Fig. 1). Ecoregions: SU, Sahelian Upwelling; MA-CI, Macaronesia–Canary Islands; SEAS, South European Atlantic Shelf; WM, western Mediterranean; CM, central Mediterranean; EM, eastern Mediterranean. The sampling gear and seagrass type found at each location is included

Authors	Location (see Fig. 1)	Ecoregion	Sampling gear	Seagrass type
Jager (1993)	Banc d'Arguin (1a)	SU	Beam trawl	Monospecific or mixed with green algae
van Etten (unpubl. data)	Banc d'Arguin (1b)	SU	Beam trawl	Monospecific
Vonk (unpubl. data)	Banc d'Arguin (1c)	SU	Fyke net and gillnet	Monospecific or mixed with <i>Zostera noltei</i>
Espino <i>et al.</i> (2011)	Lanzarote Island (2)	MA-CI	Small seine	Monospecific
Espino <i>et al.</i> (2011)	Fuerteventura Island (3)	MA-CI	Small seine	Monospecific
Espino <i>et al.</i> (2011)	Gran Canaria Island (4)	MA-CI	Small seine	Monospecific
Mena <i>et al.</i> (1993)	Tenerife Island (5)	MA-CI	Visual census	Monospecific
Ribeiro <i>et al.</i> (2006)	Ria Formosa Lagoon (6a)	SEAS	Beam trawl	Monospecific
Ribeiro <i>et al.</i> (2012)	Ria Formosa Lagoon (6b)	SEAS	Riley push net	Monospecific
Bernal (unpubl. data)	Cádiz Bay (7)	SEAS	Large seine	Monospecific
Reina-Hervás & Serrano (1987)	Málaga Bay (8)	WM	Large seine	Monospecific or mixed with green algae
Verdiell-Cubedo <i>et al.</i> (2007)	Mar Menor Sea (9)	WM	Small seine	Monospecific
Manent & Abella (2005)	Menorca Island (10a)	WM	Beam trawl	Monospecific
Manent & Abella (2005)	Menorca Island (10b)	WM	Beam trawl	Mixed with <i>Caulerpa prolifera</i>
Bussotti & Guidetti (1999)	Sardinia Island (11)	WM	Visual census	Mixed with <i>Zostera noltei</i>
Relini <i>et al.</i> (2000a, b)	Gulf of Imperia (12)	WM	Trammel net and visual census	Monospecific
Maci & Basset (2009)	Acquatina Lagoon (13)	CM	Fyke nets	Monospecific
Riccato <i>et al.</i> (2008)	Venice Lagoon (14)	CM	Small seine	Monospecific
Bonaca & Lipej (2005)	Gulf of Trieste (15)	CM	Visual census	Monospecific
Giakoumi <i>et al.</i> (2012)	Cyclades Islands (16)	EM	Visual census	Monospecific
Harmelin-Vivien <i>et al.</i> (2005)	Lebanon Coasts (17)	EM	Visual census	Monospecific
Keskin (2007)	Erdek Bay (18)	EM	Large seine	Monospecific or mixed with <i>Zostera marina</i>

2013), *i.e.* species that have their southern limit in Morocco and the Mediterranean, but not in tropical Africa; (5) tropical, species ranging from tropical west Africa to the entrance of the Mediterranean and the south of the Iberian Peninsula, or species occurring in the Red Sea and tropical west Indian ocean; (6) warm-temperate, species occurring from the Mediterranean and north-western coasts of Africa to the western entrance of the English Channel; (7) widely distributed, species present in the entire Lusitanian Province (Almada *et al.*, 2013), reaching the tropical east Atlantic Ocean, *i.e.* eurythermal species ranging from tropical to boreal areas. This last group, however, was excluded from all analyses as they do not provide any useful information for this study. For each location, the relative frequency of the above mentioned groups was calculated (Table SII, Supporting Information).

ENVIRONMENTAL AND GEOGRAPHIC DRIVERS OF AFFINITIES IN FISH COMPOSITION

A matrix of environmental and geographic data was constructed to explain macroecological similarities in assemblage composition by taking into account, for each location (Table I), the temperature (mean annual minimum and maximum) and salinity (mean annual minimum and maximum). The latitude and longitude of each location were also considered. Since the locations are situated at both sides of the 0° meridian, the longitude of each location was corrected by taking the westernmost location (Tenerife Island) as the 0° meridian (Tuya *et al.*, 2008). The new longitude of western locations was calculated as: $l_g = x_0 - x_i$; the new longitude for eastern locations as: $l_g = x_0 + x_i$ (where l_g is the corrected longitude, x_0 is the longitude of the westernmost location and x_i is the longitude of the location, both respect to the 0° meridian) (Table SIII, Supporting Information).

STATISTICAL ANALYSES

Differences in the number of families and species (*i.e.* species richness) between ecoregions were tested through the non-parametric, rank-based, Kruskal–Wallis test. Canonical analysis of principal co-ordinates (CAP; Anderson & Willis, 2003) was used as a constrained ordination procedure to test and visualize differences in fish assemblage composition between ecoregions, at the family and species level. CAP is a suitable technique to analyse biogeographic affinities in assemblage composition. Basically, CAP finds axes in the multivariate space to optimize the separation between ecoregions. First, a principal co-ordinate analysis (PCO) was carried out; CAP was then based on that sub-set of PCO axes at which additional PCO axes did not increase explanatory power. Analyses were based on Jaccard dissimilarities, which are suitable for presence–absence data (Clarke & Warwick, 2001). The trace statistic was used to test, *via* 999 permutations of the data, differences in assemblage composition, at the family and species level, between ecoregions. CAP routine also calculated miscalculation errors using the leave-one-out allocation success (LoA): each location was removed from the data set, CAP was rerun using the remaining observations and then the removed data point was classified to the nearest group centroid in the canonical space. Comparison of known with allocated groups provided miscalculation errors (Anderson & Willis, 2003). Comparisons in assemblage composition, at the family and species level, between each pair of ecoregions were carried out through a one-way ANOSIM, using 999 permutations *via* the calculation of the *R* statistic. This statistic fluctuates between –1 and 1 (*R* equals 0 if the null hypothesis is true, while values significantly different from 0 indicate some degree of discrimination). Interpretations of pair-wise *R* statistic values followed Clarke (1993). The per cent similarity (SIMPER) routine was used to identify those bioclimatic groups most contributing to explain differences in fish assemblage composition between ecoregions.

Distance-based redundancy analysis (DB-RDA; Legendre & Anderson, 1999) was used to visualize whether variation in predictor variables [environmental and geographic variables; Table SIII (Supporting Information)] explained variation in fish assemblage composition at the family and species level. Multivariate multiple regression, using the DistLM routine *via* 999 permutations of the data (Anderson, 2001), tested the significance of these relationships by fitting a linear model based on Jaccard dissimilarities. The Forward selection procedure and the Akaike information criteria (AIC) selection were applied to select the model with the

largest parsimony. Additionally, this study determined whether affinities in fish assemblage composition were related to the geographical separation between each pair of locations, by means of a correlation analysis between the pair-wise dissimilarities matrix between each pair of locations and a pair-wise matrix containing the linear distance (in km) between each pair of locations. ρ -values were calculated as Spearman rank correlations, and P -values using 999 permutations through the RELATE routine.

The occurrence of spatial serial correlation (patterns of seriation) in assemblage composition between successive ecoregions, at the family and species level, was tested through the RELATE routine. Seriation is a way to measure species turnover across space (Clarke *et al.*, 1993), *i.e.* a serial (progressive) change in assemblage composition. Seriation determines whether samples conform to a simple pattern. If seriation is significant, adjoining ecoregions are similar in composition, while the most separated ecoregions are the more dissimilar in terms of composition. Seriation analyses provide P -values, calculated *via* 999 permutations, to test for statistical significance. All multivariate procedures were carried out by means of the Primer 6 & Permanova+ package (Anderson *et al.*, 2008).

RESULTS

DESCRIPTION OF THE FISH FAUNA

The ichthyofauna associated with *C. nodosa* seagrass meadows across the Mediterranean and the adjacent Atlantic coast comprises 59 families, 113 genera and 188 species (Table SI, Supporting Information). The dominant families, in terms of species richness and frequency, are: Sparidae (20 species; present at 100% of locations), Labridae (16; 86.4%), Gobiidae (16; 90.9%), Syngnathidae (10; 86.4%), Serranidae (7; 72.7%) and Blenniidae (7; 50.0%). Other families are relevant in terms of the number of species, *i.e.* Soleidae (10 species), Carangidae (nine species), Mugilidae and Clupeidae (six species); additionally, some families are important in frequency of occurrence, *i.e.* Mullidae (77.3%), Atherinidae (68.2%), Scorpaenidae (50.0%) and Bothidae (45.5%). Only seven (11.9%) families were recorded in all ecoregions (Sparidae, Serranidae, Syngnathidae, Labridae, Gobiidae, Clupeidae and Atherinidae), and 20 (33.9%) were exclusively found in one ecoregion. The ecoregions with a larger number of families are the MA-CI (31) and the EM (30), while the CM has the least (22) [Fig. 2(a)]. Only one species, broadnose pipefish *Syngnathus typhle* L. 1758 is shared by all ecoregions; 12 species, bogue *Boops boops* (L. 1758), thicklip grey mullet *Chelon labrosus* (Risso 1827), annular seabream *Diplodus annularis* (L. 1758), sharpnout seabream *Diplodus puntazzo* (Walbaum 1792), white seabream *Diplodus sargus* (L. 1758), two-banded seabream *Diplodus vulgaris* (Geoffroy Saint-Hilaire 1817), black goby *Gobius niger* L. 1758, golden grey mullet *Liza aurata* (Risso 1810), red mullet *Mullus surmuletus* L. 1758, black scorpionfish *Scorpaena porcus* L. 1758, painted comber *Serranus scriba* (L. 1758) and black seabream *Spondyliosoma cantharus* (L. 1758) are shared by five ecoregions, whereas 91 species are restricted exclusively to one ecoregion. The ecoregion with the highest species richness is the WM (87 species), while the SU has the lowest (36 species) [Fig. 2(b)]. Significant differences in the number of families (Kruskal–Wallis ANOVA by ranks, d.f. = 5, $H = 3.005$, $P > 0.05$) and species ($H = 8.274$, $P > 0.05$) were not found between ecoregions.

AFFINITIES IN FISH COMPOSITION

At the family level, CAP [Fig. 3(a)] efficiently separates the fish assemblages from two ecoregions: the SU (LoA = 100%) and the MA-CI (LoA = 100%); the

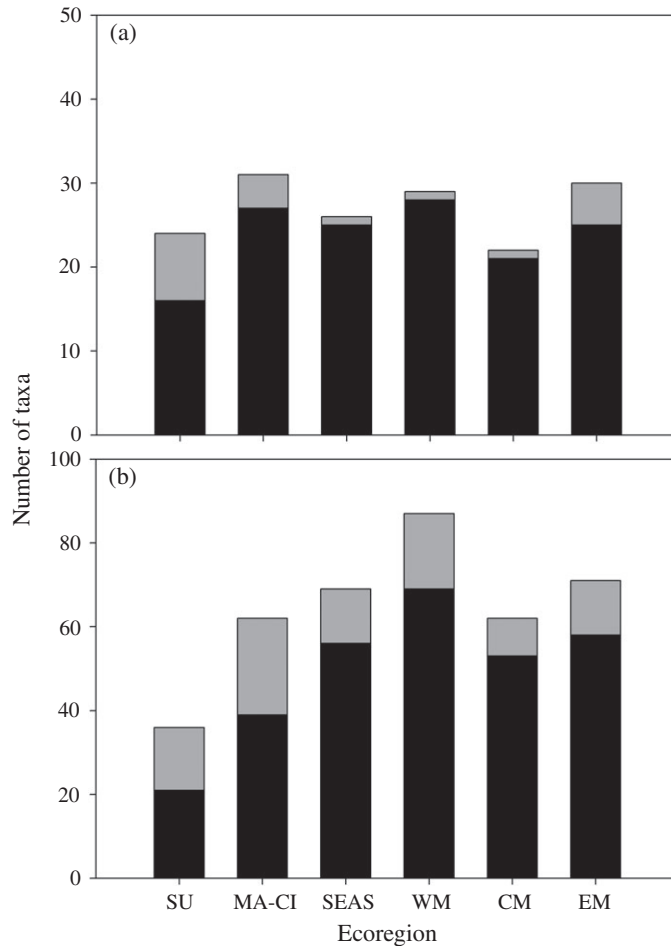


FIG. 2. Number of (a) families and (b) species at each ecoregion (■, shared taxa with any other ecoregion; ▒, unshared taxa, *i.e.* taxa exclusively found at a particular ecoregion). Ecoregions: SU, Sahelian Upwelling; MA-CI, Macaronesia-Canary Islands; SEAS, South European Atlantic Shelf; WM, western Mediterranean; CM, central Mediterranean; EM, eastern Mediterranean.

EM (LoA = 66.6%) is partially discriminated; the SEAS (LoA = 33.3%) and the WM (LoA = 33.3%) are barely separated. The CM ecoregion (LoA = 0%) is not discriminated at all. In concordance, the one-way ANOSIM shows significant overall differences in fish assemblage composition between ecoregions (global $R = 0.355$, $P < 0.01$; Table II). At the species level, CAP [Fig. 3(b)] separates the fish assemblages from the MA-CI ecoregion (LoA = 100%), while the SU (LoA = 66.7%), the SEAS (LoA = 66.7%) and the WM (LoA = 66.7%) ecoregions are partially separated; the CM (LoA = 0%) and the EM (LoA = 0%) ecoregions are not separated at all. The corresponding one-way ANOSIM shows significant differences in the species composition between ecoregions (global $R = 0.419$, $P < 0.01$; Table II). Dissimilarities in assemblage composition are connected with the geographical separation between locations at the family ($\rho = 0.197$, $P < 0.05$) and species level ($\rho = 0.264$, $P < 0.01$),

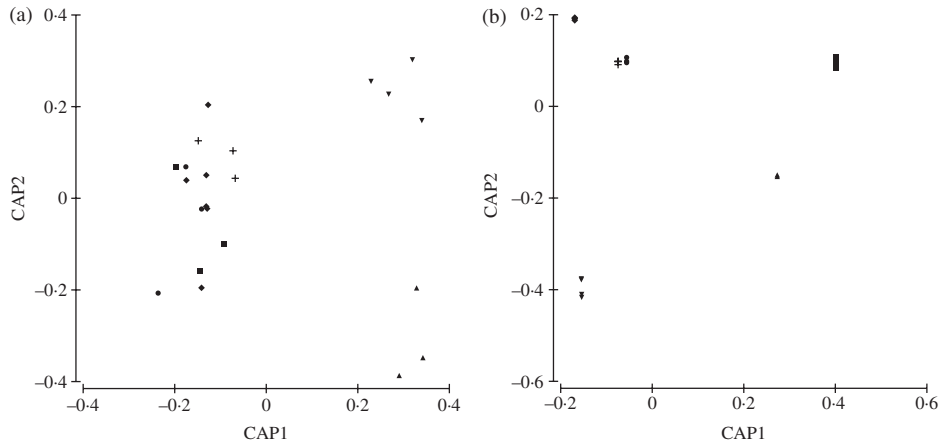


FIG. 3. Constrained canonical ordination plots (canonical analysis of principal co-ordinates, CAP) of fish assemblages inhabiting *Cymodocea nodosa* seagrass meadows according to (a) the composition of families (LoA = 54.54%, $\delta^2 = 0.97$) and (b) the composition of species (LoA = 54.55%, $\delta^2 = 0.99$). ▲, Sahelian Upwelling; ▼, Macaronesia-Canary Islands; ■, South European Atlantic Shelf; ◆, western Mediterranean; ●, central Mediterranean; +, eastern Mediterranean. Analyses were based on five and 11 principal co-ordinate analysis (PCO) axes, respectively. LoA, leave-one-out allocation success (*i.e.* the percentage of points correctly allocated into each group); δ^2 , square canonical correlation with CAP I.

respectively. A significant spatial serial correlation in fish assemblage composition was detected between ecoregions along the distribution range of *C. nodosa*, at the family and species level ($\rho = 0.292$, $P < 0.001$; $\rho = 0.411$, $P < 0.001$, respectively).

The bioclimatic classification of fish assemblages shows that 50.5% of the total species are widely distributed, followed by temperate (16.0%), tropical (14.4%), Mediterranean (8.5%), warm-temperate (7.5%), Macaronesian (2.7%) and cold-temperate (1.1%) species. The results of the SIMPER routine (Table III) show that temperate, Mediterranean and warm-temperate species mostly contribute to dissimilarities between the SEAS, WM, CM and EM ecoregions (Fig. 4). Tropical, temperate and Macaronesian species mostly explain dissimilarities between the SU and the MA-CI ecoregions. Temperate and tropical species for the SU and tropical, temperate and Macaronesian species for the MA-CI are majorly responsible of dissimilarities between these two ecoregions and the temperate ecoregions (SEAS, WM, CM and EM), respectively (Fig. 4).

ENVIRONMENTAL AND GEOGRAPHIC DRIVERS OF AFFINITIES IN FISH COMPOSITION

The first two axes from the DB-RDA explain *c.* 25.7 and 24.0% of the total variation in the fish assemblage composition at the family and species level, respectively (Fig. 5). The mean annual minimum seawater temperature is the environmental factor that explains most variation in fish assemblage composition at the family and species level, *c.* 15 and 14% of the total variation ($P < 0.001$ in both cases; Table IV), respectively. The second factor that most contributes to explain variation in fish assemblage composition is latitude, *c.* 10 and 9% of the total variation, respectively, at the family and species level ($P < 0.01$ in both cases; Table IV).

TABLE II. One-way ANOSIM testing for differences in fish assemblage composition between each pair of ecoregions at the family and species levels

Pair-wise comparison	Family		Species	
	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>
SU v. MA-CI	0.880	<0.05	0.759	<0.05
SU v. SEAS	0.907	>0.05	0.722	>0.05
SU v. WM	0.522	<0.05	0.762	<0.05
SU v. CM	0.870	>0.05	0.815	>0.05
SU v. EM	0.778	>0.05	0.833	>0.05
MA-CI v. SEAS	0.815	<0.05	1.000	<0.05
MA-CI v. WM	0.407	<0.05	0.573	<0.05
MA-CI v. CM	0.981	<0.05	0.944	<0.05
MA-CI v. EM	0.472	<0.05	0.935	<0.05
SEAS v. WM	-0.117	>0.05	-0.130	>0.05
SEAS v. CM	-0.074	>0.05	0.074	>0.05
SEAS v. EM	0.352	>0.05	0.185	>0.05
WM v. CM	-0.194	>0.05	-0.241	>0.05
WM v. EM	0.127	>0.05	-0.176	>0.05
CM v. EM	0.333	>0.05	-0.130	>0.05

SU, Sahelian Upwelling; MA-CI, Macaronesia-Canary Islands; SEAS, South European Atlantic Shelf; WM, western Mediterranean; CM, central Mediterranean; EM, eastern Mediterranean.

DISCUSSION

DESCRIPTION OF THE FISH FAUNA: PATTERNS IN THE NUMBERS OF FAMILIES AND SPECIES

The absence of patterns for the species richness of fish assemblages throughout the distribution range of *C. nodosa* follows previous results for seagrass-associated ichthyofauna. In this sense, the review by Pollard (1984) did not find any general pattern for the species richness of 30 fish assemblages from all over the world; differences in species richness mostly reflected differences in sampling efforts and techniques between locations. The larger number of fish species associated with *C. nodosa* meadows was observed at the WM, where there has been considerable sampling effort, as a result of the long tradition in marine biological studies (Table I). Similarly, the number of families does not show any particular pattern, which might be due to the different sampling protocols and sampling efforts between locations. For example, the ecoregions with the larger number of families (MA-CI and EM) are those where a combination of sampling strategies, visual censuses and bottom trawls, in particular, was carried out. A relevant element that also influences fish species richness is the landscape ecology of seagrass meadows, *e.g.* the identity and proximity from surrounding habitats (Weinstein & Heck, 1979; Costa *et al.*, 2002; Lugendo *et al.*, 2005; Jelbart *et al.*, 2007; Unsworth *et al.*, 2008; Tuya *et al.*, 2010), as well as the structural complexity of seagrass meadows. All of these landscape attributes operating at medium and small scales have been ignored by the present macroecological approach as this information is lacking for most studies, especially for *C. nodosa* (Boström *et al.*, 2006).

TABLE III. Results of the SIMPER routine indicating those bioclimatic fish categories (ct, cold-temperate; mc, Macaronesian; md, Mediterranean; t, temperate; tp, tropical; wt, warm-temperate) mostly contributing to dissimilarities between each pair of ecoregions. The groups are in decreasing order of contribution

SU v. MA-CI $\bar{\delta}i = 51.22$		SU v. SEAS $\bar{\delta}i = 81.46$		MA-CI v. SEAS $\bar{\delta}i = 69.37$		SU v. WM $\bar{\delta}i = 79.38$		MA-CI v. WM $\bar{\delta}i = 65.06$		SEAS v. WM $\bar{\delta}i = 36.76$	
Groups	$\bar{\delta}i\%$	Groups	$\bar{\delta}i\%$	Groups	$\bar{\delta}i\%$	Groups	$\bar{\delta}i\%$	Groups	$\bar{\delta}i\%$	Groups	$\bar{\delta}i\%$
tp	31.02	t	49.05	tp	30.86	t	38.71	tp	44.69	t	47.92
t	30.84	tp	21.51	t	27.49	tp	34.43	mc	18.91	wt	23.24
mc	27.82	wt	19.48	wt	19.31	wt	16.32	wt	15.02	md	10.10
wt	10.32	-	-	mc	13.60	md	10.53	t	12.96	ct	9.42
-	-	-	-	-	-	-	-	-	-	-	-
SU v. CM $\bar{\delta}i = 88.10$		MA-CI v. CM $\bar{\delta}i = 73.57$		SEAS v. CM $\bar{\delta}i = 22.86$		WM v. CM $\bar{\delta}i = 31.98$		SU v. EM $\bar{\delta}i = 69.26$		MA-CI v. EM $\bar{\delta}i = 67.26$	
Groups	$\bar{\delta}i\%$	Groups	$\bar{\delta}i\%$	Groups	$\bar{\delta}i\%$	Groups	$\bar{\delta}i\%$	Groups	$\bar{\delta}i\%$	Groups	$\bar{\delta}i\%$
t	42.51	tp	33.28	t	34.41	t	45.74	tp	36.85	tp	34.73
tp	24.64	t	22.60	md	31.83	md	26.72	t	32.24	t	22.08
md	17.30	wt	15.93	ct	12.35	wt	21.29	wt	18.11	mc	17.26
wt	15.54	md	15.03	wt	11.30	wt	1.16	md	12.80	wt	15.98
-	-	mc	13.16	tp	10.11	tp	0.66	-	-	-	-
SEAS v. EM $\bar{\delta}i = 48.28$		WM v. EM $\bar{\delta}i = 49.55$		CM v. EM $\bar{\delta}i = 44.95$							
Groups	$\bar{\delta}i\%$	Groups	$\bar{\delta}i\%$	Groups	$\bar{\delta}i\%$						
t	52.81	t	1.73	t	1.83						
wt	14.04	wt	1.06	wt	1.42						
tp	13.96	tp	0.95	tp	0.88						
md	12.44	md	1.44	md	1.56						
-	-	-	-	tp	12.85						
-	-	-	-	wt	12.86						
-	-	-	-	md	19.59						
-	-	-	-	t	54.69						
-	-	-	-	-	1.95						

$\bar{\delta}i$, mean dissimilarity; $\bar{\delta}i\%$, contribution of each bioclimatic fish category to dissimilarities. Ecoregions: SU, Sahelian Upwelling; MA-CI, Macaronesia-Canary Islands; SEAS, South European Atlantic Shelf; WM, western Mediterranean; CM, central Mediterranean; EM, eastern Mediterranean.

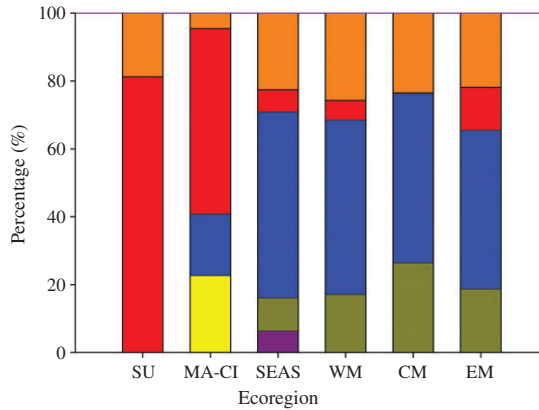


FIG. 4. Composition of fish assemblages inhabiting *Cymodocea nodosa* seagrass meadows at each ecoregion according to the bioclimatic affinities of fish species (■, cold-temperate; □, Macaronesian; ■, Mediterranean; ■, temperate; ■, tropical; ■, warm-temperate). Ecoregions: SU, Sahelian Upwelling; MA-CI, Macaronesia-Canary Islands; SEAS, South European Atlantic Shelf; WM, western Mediterranean; CM, central Mediterranean; EM, eastern Mediterranean.

The dominant fish families associated with *C. nodosa* meadows (Sparidae, Labridae, Gobiidae, Syngnathidae, Blenniidae and Scorpaenidae) have also been identified as conspicuous families inhabiting seagrass meadows at global scales (Pollard, 1984). Still, some fish families (*e.g.* Soleidae, Mullidae and Atherinidae) that are important in *C. nodosa* meadows, either in terms of number of species or frequency of appearance, have been previously neglected as important taxonomic elements of the fish fauna inhabiting seagrass meadows at global scales.

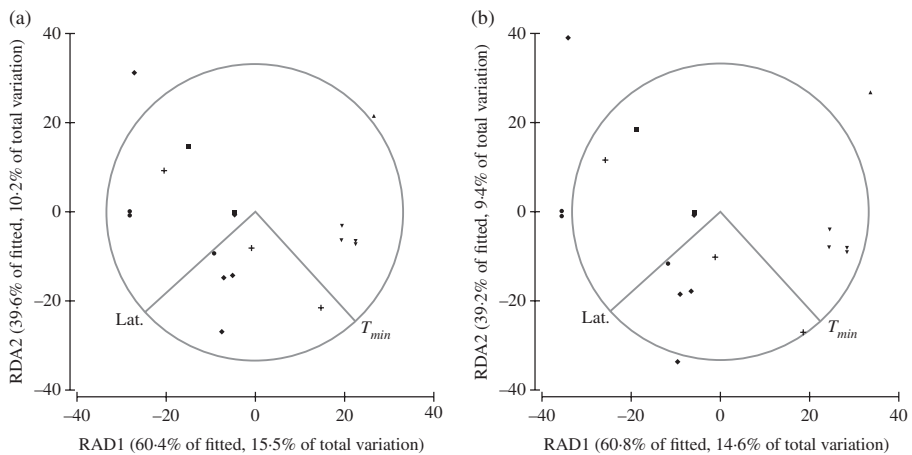


FIG. 5. Distance-based redundancy analysis (DB-RDA) biplots of first and second axes relating environmental and geographic variables to the composition of fish assemblages inhabiting *Cymodocea nodosa* seagrass meadows at the level of (a) families and (b) species. ▲, Sahelian Upwelling; ▼, Macaronesia-Canary Islands; ■, South European Atlantic Shelf; ◆, western Mediterranean; ●, central Mediterranean; +, eastern Mediterranean; T_{min} , minimum mean annual temperature; Lat., latitude.

TABLE IV. Results of multivariate multiple regression models (sequential tests) testing relationships between environmental and geographic variables and the composition of fish assemblages inhabiting *Cymodocea nodosa* seagrass meadows at the family and species levels. The contribution of each independent variable is described by means of the amount (%) of explained variation, and *P*-values provide significance diagnoses

Variables	Families level			Species level		
	Pseudo- <i>F</i>	<i>P</i>	% explained variation	Pseudo- <i>F</i>	<i>P</i>	% explained variation
Mean minimum temperature	3.6673	<0.001	0.15495	3.4237	<0.001	0.14616
Latitude	2.6001	<0.01	0.10172	2.3541	<0.01	0.09413

AFFINITIES IN THE COMPOSITION OF THE FISH FAUNA

The composition of the fish fauna inhabiting *C. nodosa* seagrass meadows, at the family and species level, differs throughout the distribution range of the seagrass. The general pattern is a progressive change from the tropical ecoregion (SU) towards the subtropical Macaronesian ecoregion (MA-CI) and the four temperate ecoregions (SEAS, WM, CM and EM); variation in fish composition within these ecoregions is, however, minor. A range of studies have reported changes in ecological attributes of marine fishes across latitudinal and longitudinal gradients, which are connected with oceanographic and climatic patterns, *e.g.* latitudinal changes in species richness and the size of species distribution ranges (Macpherson & Duarte, 1994; Macpherson, 2002; Lasram *et al.*, 2009), fish diversity (Briggs, 1995; Willig *et al.*, 2003; Tuya *et al.*, 2011, 2012) and the trophic structure and mobility of fishes (Floeter *et al.*, 2004).

The composition of the fish fauna within the SU ecoregion differs as a result of the presence of taxa of tropical affinity (*e.g.* Ariidae, Cichlidae, Ephippidae, Haemulidae, Monacanthidae, Polynemidae, Psettodidae and Tetraodontidae); indeed, one third of the families observed at the SU are exclusively found here. Similarly, numerous fish species (28.6%) of tropical distribution are exclusive to this ecoregion, in particular marbled stingray *Dasyatis marmorata* (Steindachner 1892), smoothmouth sea catfish *Carlarius heudelotii* (Valenciennes 1840), rough-head sea catfish *Arius latiscutatus* Günther 1864, *Enneacampus kaupi* (Bleeker 1863), prickly puffer *Ephippion guttifer* (Bennett 1831), East Atlantic African spadefish *Ephippus gorensis* Cuvier 1831, bonga shad *Ethmalosa fimbriata* (Bowdich 1825), lesser African threadfin *Galeoides decadactylus* (Bloch 1795), cyclope sole *Solea triophthalma* Bleeker 1863, spot-tail spiny turbot *Psettodes belcheri* Bennett 1831 and Guinean tilapia *Coptodon guineensis* (Günther 1862); or shared with the MA-CI, *e.g.* bastard grunt *Pomadasys incisus* (Bowdich 1825), Guinean puffer *Sphoeroides marmoratus* (Lowe 1838) and planehead filefish *Stephanolepis hispidus* (L. 1766). Some warm-temperate species are also shared with the SEAS, *e.g.* Senegal seabream *Diplodus bellottii* (Steindachner 1882) and Senegalese sole *Solea senegalensis* Kaup 1858. This particular composition of the ichthyofauna of the SU is the result of the location of this ecoregion within the West African Transition province, so a different biota is expected relative to the Lusitanian and Mediterranean provinces, according with Spalding *et al.* (2007). The composition of the fish fauna inhabiting *C. nodosa* meadows in the SU is, therefore, dominated by tropical elements that reach here their northern distribution edge (*e.g.*

E. goreensis), while some temperate species have here their southern distribution limit [e.g. Baillon's wrasse *Symphodus bailloni* (Valenciennes 1839) (Jager, 1993)].

The MA-CI ecoregion shows the largest dissimilarities in fish composition with the rest of the ecoregions. At the family level, differences are mostly related to the presence of taxa of tropical affinity (Aulostomidae, Haemulidae, Monacanthidae, Pomacentridae, Scaridae and Tetraodontidae), some of them also found in the SU. At the MA-CI, there is a coexistence of species of tropical affinities, in particular Atlantic cornetfish *Aulostomus strigosus* Wheeler 1955, leopard eel *Myrichthys pardalis* (Valenciennes 1839), the clingfish *Opeatogenys cadenati* Briggs 1957, Madeira rockfish *Scorpaena maderensis* Valenciennes 1833, Yellowmouth barracuda *Sphyaena viridensis* Cuvier 1829, fusca drum *Umbrina ronchus* Valenciennes 1843, pearly razorfish *Xyrichtys novacula* (L. 1758), *P. incisus*, *S. marmoratus*, parrotfish *Sparisoma cretense* (L. 1758), ornate wrasse *Thalassoma pavo* (L. 1758), Macaronesian sharpnose-puffer *Canthigaster capistrata* (Lowe 1839) and *S. hispidus*, subtropical species, diamond lizardfish *Synodus synodus* (L. 1758) and species endemic to the Macaronesia, such as Canary damsel *Similiparma lurida* (Cuvier 1830), comb or island grouper *Myceteroperca fusca* (Lowe 1838) and emerald wrasse *Symphodus trutta* (Lowe 1834). The presence of tropical fish taxa in the nearshore waters of the Canary Islands is prominent (Brito *et al.*, 2005). This archipelago has a tropicalization index (5.56, *i.e.* the percentage contribution of tropical species to the entire fish assemblage; Wernberg *et al.*, 2013) rather superior relative to the Atlantic Iberian Peninsula (1.13) and the Mediterranean Sea (1.6) (Almada *et al.*, 2013). Some temperate species, *e.g.* *D. annularis* and *S. porcus*, are shared with temperate ecoregions. The biogeographic composition of the littoral ichthyofauna of the Canary Islands is explained by the peculiar oceanographic conditions of this archipelago, located across the north-western African upwelling transition zone. There is a gradient in ocean climate across an east to west axis perpendicular to the African coast. As a result, there is, for example, an average of 2°C difference in sea surface temperature between the eastern and westernmost islands (Davenport *et al.*, 2002). In turn, marine biota differ between the eastern and westernmost islands, including the structure and composition of nearshore fish assemblages (Brito *et al.*, 2005; Tuya *et al.*, 2006), which explains the confluence of tropical and warm-temperate species in the archipelago.

For the two taxonomic levels considered here, there is no significant difference in the composition of the fish fauna among the temperate ecoregions (SEAS, WM, CM and EM). At the family level, SEAS, WM and CM have a very similar composition; *i.e.* most taxa are shared. The EM, however, partially differs from this group as a result of the presence of fish families of tropical distribution (Monacanthidae, Pomacentridae, Scaridae and Siganidae; 16.7% of exclusive taxa). Despite the fact that CAP, at the species level, reveals some differences in fish composition between the SEAS and WM, the results are not significant. This fact does not fit with the model outlined by Spalding *et al.* (2007). This, of course, may be an artefact of the lack of data from the SEAS, CM and EM in Spalding *et al.*'s (2007) analysis. The Strait of Gibraltar has been largely considered as a natural border between the Mediterranean and the Atlantic (Briggs & Bowen, 2012); genetic evidence for some coastal fish species supports this notion. Yet, there is no general consensus on the pivotal role that the Strait of Gibraltar plays in the configuration of phylogenetic patterns of marine fishes (Bargelloni *et al.*, 2003, 2005; Patarnello *et al.*, 2007). The slight difference in fish composition between the SEAS and the adjacent WM results from the presence of cold-temperate species,

e.g. ballan wrasse *Labrus bergylta* Ascanius 1767 and worm pipefish *Nerophis lumbriciformis* (Jenyns 1835) and tropical species, *e.g.* African halfbeak *Hyporhamphus picarti* (Valenciennes 1847) that reach their southern and northern distribution range edges at the SEAS, respectively. In this ecoregion, the dominant climatic groups are those of temperate affinity, including species also present across the Mediterranean, *e.g.* goldsinney wrasse *Ctenolabrus rupestris* (L. 1758), lesser weever *Echiichthys vipera* (Cuvier 1829), painted goby *Pomatoschistus pictus* (Malm 1865), shi drum *Umbrina cirrosa* (L. 1758), pointed-snout wrasse *Symphodus scina* (Fabricius 1775) and ocellated wrasse *Symphodus ocellatus* (L. 1758). The exchange of species between these two sectors (SEAS and WM) of the Lusitanian province has already been previously indicated (Bianchi, 2007; Tuya *et al.*, 2012; Almada *et al.*, 2013).

The ichthyofauna living in *C. nodosa* meadows from the WM ecoregion has largely been described; this fish fauna is typically dominated by species of temperate affinity, *e.g.* twaite shad *Alosa fallax* (Lacépède 1803), crystal goby *Crystallogobius linearis* (Düben 1845), Bucchich's goby *Gobius bucchichi* Steindachner 1870, turbot *Scophthalmus rhombus* (L. 1758) and blotched picarel *Spicara maena* (L. 1758), and Mediterranean distribution, *e.g.* scaldback *Arnoglossus kessleri* Schmidt 1915, Spanish toothcarp *Aphanius iberus* (Valenciennes 1846), combtooth blenny *Microlipophrys dalmatinus* (Steindachner & Kolombatovic 1883) and *Symphodus doderleini* Jordan 1890. Some elements of tropical, *e.g.* Adriatic sole *Pegusa impar* (Bennett 1831), and warm-temperate, *e.g.* cline *Clinitrachus argentatus* (Risso 1810), affinities are also found here. Despite the WM being a fish diversity hotspot, including a number of endemics (Lasram *et al.*, 2009; Coll *et al.*, 2010), only one species (*A. iberus*) inhabiting *C. nodosa* meadows is endemic from this ecoregion. The CM is the least differentiated and diverse (in terms of species richness) ecoregion, with a lack of tropical elements. This may be explained by, firstly, the location of this ecoregion between the WM and EM, sharing a large number of species with both ecoregions. Secondly, this ecoregion is under oceanographic conditions characterized by low winter seawater temperatures (10° and 14° in the northern and southern Adriatic Sea, respectively; Bianchi, 2007), which creates a thermal barrier for tropical species. A large number of fish species are endemic to this part of the Mediterranean (Lasram *et al.*, 2009; Coll *et al.*, 2010). Only one endemic fish species that lives in *C. nodosa* meadows, however, has been found in this ecoregion; the gobiid Adriatic dwarf goby *Knipowitschia panizzae* (Verga 1841), which is restricted to the Adriatic and Tyrrhenian Seas. Overall, this study shows the Mediterranean ecoregions have a level of endemism (12-69%) similar to those previously indicated for the Mediterranean Sea (Coll *et al.*, 2010; Briggs & Bowen, 2012; Almada *et al.*, 2013).

The composition of the fish fauna in the EM is influenced by the influx of tropical species that have performed Lessepsian migrations through the Suez Channel towards the Mediterranean (Bianchi, 2007; Golani, 2010; Coll *et al.*, 2010). For example, reticulated leatherjacket *Stephanolepis diaspros* Fraser-Brunner 1940, dusky spinefoot *Siganus luridus* (Rüppell 1829) and marbled spinefoot *Siganus rivulatus* Forsskål & Niebuhr 1775, which originate from the Indian Ocean, have been registered in *C. nodosa* meadows on the Lebanese coast (Harmelin-Vivien *et al.*, 2005). Another example is bluespotted cornetfish *Fistularia commersonii* Rüppell 1838 (Fistulariidae), which use *C. nodosa* meadows as nursery habitats in the Aegean Sea (Kalogirou *et al.*, 2007). Another set of species of tropical affinities observed in the EM includes *S. cretense* and *X. novacula* (Harmelin-Vivien *et al.*, 2005).

INFLUENCE OF ENVIRONMENTAL AND GEOGRAPHIC VARIABLES

The distribution of marine fishes at macroecological scales is complex, including a range of processes that affect their distribution (*e.g.* temperature, salinity, primary productivity, geologic history and past climatic events and larval dispersion) (Briggs, 1974, 1995; Floeter *et al.*, 2008). In this study, a gradient in the mean minimum annual temperature of *c.* 6.5° C between the tropical zone (19.88° N) and the temperate north-eastern Atlantic (36.98° N) partly explains variation in the composition of the fish assemblage at the family and species level. This temperature gradient, to some extent, is connected with latitude. It has been largely recognized that seawater temperature influences the distribution pattern of nearshore fishes and creates variation in the richness, diversity and abundance of fish assemblages (Tuya *et al.*, 2011, 2012). In the Mediterranean Sea, variation of seawater temperature does not follow a straightforward pattern, despite, in general, the minimum annual seawater temperature presenting a north-west to south-east gradient of *c.* 7° C (Bianchi, 2007; Coll *et al.*, 2010). This fact may help explain the presence of tropical taxa in the south-east sector of the Mediterranean and the dominance of temperate taxa in the north-west. Despite the fact that the multivariate regression model excluded variation in longitude from the model with the largest parsimony, variation across longitude explains a small amount of variation in the composition of the fish fauna (*c.* 8 and 9% at the family and species level, respectively); this is probably associated with the turnover of species with longitude across the Mediterranean.

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Supporting Information

Supporting Information may be found in the online version of this paper:

Table SI Presence–absence matrices at the level of family and species for each location within each ecoregion

Table SII Matrix of fish bioclimatic categories for each location within each ecoregion

Table SIII Matrix of environmental and geographical data for each location within each ecoregion

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