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## Multi-scale spatial heterogeneity, habitat structure, and the effect of marine reserves on Western Mediterranean rocky reef fish assemblages

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**Abstract** A hierarchical sampling design, spanning five orders of magnitude (from 10s of metres to 100s of kilometres) was created in order to quantify the multi-scale spatial variability of visually censused rocky reef fish assemblages in the western Mediterranean Sea. Specifically, we tested the hypotheses that species abundance and the biomass of reef fish populations is higher within than outside marine reserves, and that a north-to-south geographical gradient of these variables exists. We also explored the relationship between the fish assemblage and habitat structure, as an environmental factor likely to account for an important part of the observed variability. The mixed analyses of variance revealed that total abundance and biomass, species richness and abundance and biomass of several target species reached higher average values within marine reserves. Nevertheless, some non-protected localities (e.g. Aguilas) harboured richer and more abundant fish

assemblages than some marine reserves. In addition, regional variation, attributable to differences in local carrying capacity and hydroclimatic conditions, are also shown across the studied area. Moreover, the studied assemblage is patchy at small and/or intermediate spatial scales, considering both assemblage descriptors (total abundance and biomass, species richness), and the abundance and biomass of fish species and spatial categories. Detected patterns were different depending on the species and assemblage variables analysed. Differences in habitat structure account for a significant proportion of total variability of the studied variables, and are likely to be responsible for a large part of the observed differences, especially at small-to-intermediate spatial scales. Other factors—spatial variability in larval distribution, settlement and/or post-settlement survival—are discussed in order to explain the observed differences. We concluded that causes of the observed patchiness of Mediterranean reef fish assemblages are probably multiple. Long-term, multi-scale spatial and temporal monitoring actions, as well as process-oriented manipulative experiments are urgently needed in order to ascertain the relative importance of each factor.

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### Introduction

It is widely acknowledged that ecological communities are patchy, this patchiness being evident at several, often simultaneous, spatial and temporal scales (Dayton and Tegner 1984; Kotliar and Wiens 1990). The study of spatial pattern is crucial as a first step to understanding the causes of the distribution and abundance of organisms (Levin 1992), and to provide a basis for monitoring their long-term changes due to both natural and human disturbances (Underwood 1990). The multi-scale nature of patchiness of reef fish assemblages has been widely described in coral reefs (e.g. Williams and Hatcher 1983; Russ 1984a, 1984b; Galzin 1987; Williams 1991; Roberts et al. 1992; Galzin et al. 1994; Cadoret et al. 1999; Holbrook et al. 2000; Gust et al. 2001). In contrast,

studies aiming to ascertain the multi-scaled pattern of natural variation in space and/or time of temperate fish assemblages are lacking. Previous studies in the Mediterranean Sea have documented reef adult fish assemblage structure in particular locations (usually protected from fishery) (Harmelin 1987; Spyker and van den Berghe 1995; Reñones et al. 1997; García Charton and Pérez Ruzafa 1998, 2001; La Mesa and Vacchi 1999; Mouillot et al. 1999). Recruitment of reef fishes has also been reported to be variable at several, simultaneous spatial scales in coral reefs (e.g. Lincoln Smith et al. 1991; Fowler et al. 1992; Planes et al. 1993) and in the Mediterranean littoral (Macpherson et al. 1997; Vigliola et al. 1998).

Observed spatial and temporal variability in abundance of adult reef fish assemblages have been attributed to different biological and/or physical factors (Jones 1991), including variations in depth (Bell 1983; Harmelin 1990; McGehee 1994; García-Charton and Pérez-Ruzafa 1998); habitat structure—resulting in differential availability of resources such as food or shelter (García-Charton et al. 2000); climatic differences (Holbrook et al. 1997); predation (Hixon 1991); competition (Sale 1978; Gladfelter et al. 1980); episodic disturbances (Walsh 1983; Chabanet et al. 1995); larval dynamics (Leis and McCormick 2002); and recruitment variability (Booth and Brosnan 1995). Each factor would act preferentially at particular spatial scales (Sale 1998). A number of studies have explored the effect of the cessation of fishing within marine reserves, as a human factor likely to greatly influence fish communities, and found that, in general, the abundance, biomass and mean size of exploited fish populations are higher within protected areas than in nearby non-reserve areas, both in the Mediterranean (Bell 1983; García-Rubies and Zabala 1990; Francour 1994; Harmelin et al. 1995) and elsewhere (Russ 2002; Halpern 2003). Nevertheless, some studies have found little, if any, differences between protected and fished areas (e.g. Samoily 1988; Roberts and Polunin 1992; Dufour et al. 1995), which are probably linked to the methodological problems raised by the need to distinguish natural spatial and temporal variability of fish assemblages from the effects of management measures (García-Charton and Pérez-Ruzafa 1999; García-Charton et al. 2000).

However, the study of spatial pattern of fish communities, as other organisms, is constrained by the fact that spatial scale of observation is a methodological decision of the observer rather than an intrinsic feature of ecological processes (Allen and Hoekstra 1991). Observed patterns can be different depending on the scale of observation (Hewitt et al. 1998), but also a variety of factors could be jointly responsible for the same pattern observed at a specific scale (Jones 1991). These factors will differ in the intensity of their effects, i.e. their relative importance (Steele 1997), and in the domain of scale in which they act preferentially (Wiens 1989). As a consequence of the multiplicity of factors potentially determining the observed spatial patchiness, an optimal

strategy consists in studying the patterns of interest at multiple, simultaneous scales, identifying relevant scales of natural variability, and then listing a series of hypotheses and testing them to account for the observed patterns. This inductive procedure (from effects to causes), however, is less conclusive than the hypothetic-deductive method—based on experimental manipulations (Sale 1984; Underwood 1997), but it is the only practicable way to ascertain the influence of factors acting at large spatial scales.

Here we examine the distribution and abundance patterns of the fish assemblage inhabiting the rocky reefs in the western Mediterranean Sea, over spatial scales spanning five orders of magnitude ( $10^1$ – $10^5$  m), in order to quantify population variability, and to catalogue hypotheses on factors likely to account for this observed variability. Particularly, we test the hypothesis that species abundance and biomass of rocky reef fish populations are higher within than outside Mediterranean marine reserves. To do so, we used replicate visual censuses randomly located following a mixed sampling design that included marine reserves protected from fishing and non-protected areas. This approach allows variability to be assessed simultaneously at a hierarchy of spatial scales, so that the scales that contributed most to total variation can be identified (Underwood 1997). Furthermore, we explore the relationship between the fish assemblage and habitat structure, as an environmental factor likely to account for an important part of the observed variability.

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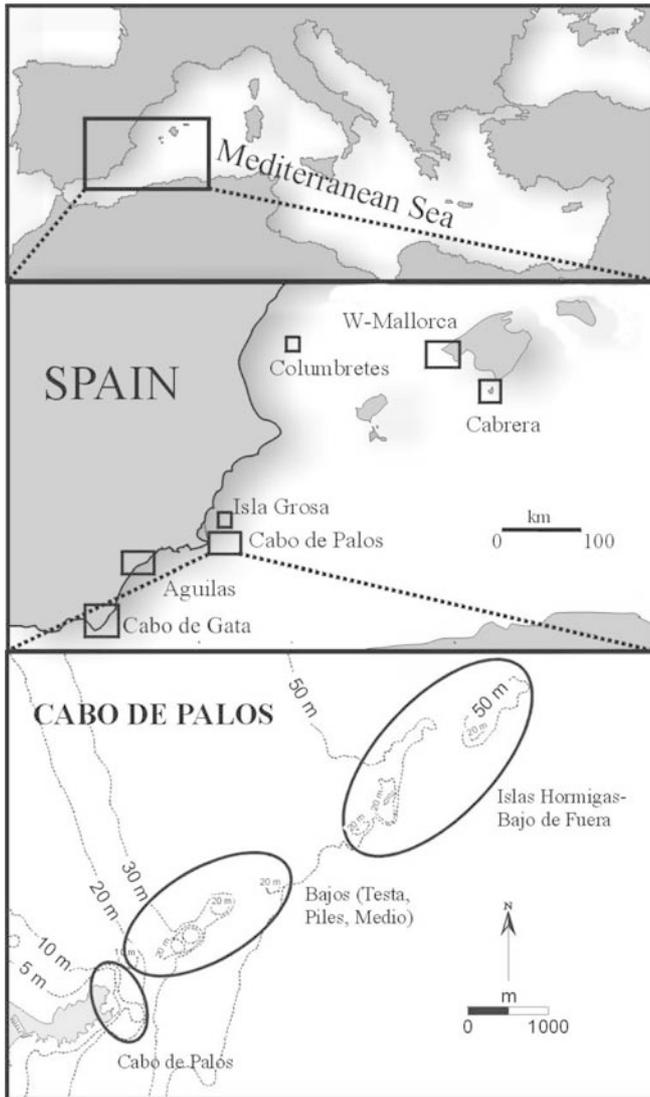
## Materials and methods

### Sampling design

This study incorporated four spatial scales, from 10s of metres among replicate transects, to 10s to 100s of kilometres among localities. Thus, between June and October 1996, seven localities were surveyed in the western Mediterranean, encompassing a geographic range of about 400 km of latitude by about 500 km of longitude—from South to North: Cabo de Gata, Águilas, Cabo de Palos, Isla Grosa, Cabrera, Western-Mallorca and Columbretes (Fig. 1; Table 1). In four of these localities some measures of protection from fisheries were in force at the time of sampling (see Table 1 for details). Then, we randomly selected three sectors covering an area of about 20 to 50 ha each, and situated 1,000s of metres apart within each locality, whether protected or not (Fig. 1); three zones 2–5 ha large (separated by 100s of metres within each sector), and within each zone, we located (again randomly) three replicate 50×5-m transects, along which we censused fishes visually and measured a series of habitat descriptors (see below). The only conditions for locating the 189 resulting transects were to maintain as much as possible a similar depth (10–12 m), and a predominantly rocky bottom.

### Fish counts and habitat measurements

Fish assemblages were visually surveyed by a SCUBA diver along each 50×5-m transect using a tape measure and recording in an underwater-notebook the abundances and individual sizes for each species encountered. Several observers participated in the sampling operations, after several training sessions. Previous work (C. Valle, J. Bayle, J.A. García-Charton and D. Moreno, unpublished data)



**Fig. 1** Location of the studied localities in the western Mediterranean Sea, showing the three sectors within the Cabo de Palos–Islas Hormigas Marine Reserve as an example of the spatially hierarchical sampling design adopted in the present study

**Table 1** Description of the seven localities studied. The four protected localities include integral-reserve zones (where all activities are banned), and buffer zones (where recreational and commercial fishing, mooring and diving are regulated). Month of the year when sampling was done at each locality is also shown

Locality	Geographical co-ordinates	Type of coast	Sectors	Protection?	Period of sampling in 1996
Cabo de Gata	36° 42'N 2° 11'W	Mainland	Loma Pelada, Punta Javana–S. Pedro, Cabo de Gata–La Laja	12,200 ha protected since 1987	October
Aguilas	37° 24'N 1° 34'W	Mainland	El Fraile–La Pava, Calabardina–La Yesera, La Fuente–La Cruz	None	September
Cabo de Palos	37° 38'N 0° 42'W	Mainland/ inshore islands	Cabo de Palos, Bajos, Islas Hormigas	1,898 ha protected since 1995	August
Isla Grosa	37° 47'N 0° 43'W	Inshore islands	Farallón–La Laja, Isla Grosa, Barra	None	August
Cabrera	39° 10'N 2° 58'E	Inshore islands	Rates, L'Imperial–Ses Bledes, Foradada	8,703 ha protected since 1991	June
W-Mallorca	39° 30'N 2° 30'E	Mainland	Andraitx, Dragonera, Estellencs	None	June
Columbretes	39° 52'N 0° 43'E	Offshore islands	Illa Grossa, Bergantín, Foradada	4,000 ha protected since 1990	June

showed that fish counts, size estimations and habitat measurements did not differ significantly among trained observers. Small-sized, cryptic species (belonging to families Gobiidae, Callyonimidae, Bleniidae, Gobiosocidae and Tripterygiidae) were excluded from the censuses to avoid biases (García-Charton and Pérez-Ruzafa 2001). Each observation was assigned to one of nine predetermined abundance classes proposed by Harmelin (1987), the limits of which coincide with the terms of a base-2 geometric series. Geometric means of each fish abundance class were used for calculations. The size of individuals (in classes of 2 cm) was visually estimated after a training period (Bell et al. 1985). All censuses were done between 1000 and 1500 hours, when water conditions (turbidity and swell) were optimal (Harmelin-Vivien et al. 1985).

When considering the variables describing the habitat structure, we distinguished between vertical complexity (estimated as number of rocky boulders and verticality) and horizontal heterogeneity (García-Charton and Pérez-Ruzafa 1998, 2001). After counting fishes, the same observer covered the transect length in the opposite direction to count the number of rocky boulders classified by the size of their major length (ML)—small ( $ML \leq 1$  m), medium ( $1 \text{ m} < ML \leq 2$  m), and large ( $ML > 2$  m). Finally, the observer completed a third run to measure the depth every 5 m along the transect—in order to obtain the average depth—and habitat heterogeneity, estimated visually as the relative percentage cover of different substrate types—rock, clumps of *Posidonia oceanica* over rock, and patches of sand—within each transect. Verticality was estimated as the vertical distance (in metres) between the deepest and the shallowest point inside each transect.

#### Data analysis

Fish assemblage structure was specified for each transect by species richness, abundance (total, and excluding pelagic, shoaling species),  $H'$ , Shannon–Wiener's diversity index and species composition. For each species we estimated its relative abundance and frequency of occurrence, classifying them as very frequent ( $f \geq 70\%$ ), frequent ( $40\% \leq f < 70\%$ ), common ( $15\% \leq f < 40\%$ ) and occasional species ( $f < 15\%$ ). Fish species biomass was estimated from the abundance data by size-classes within each transect, using weight–length relationships calculated from experimental and commercial fishing data obtained in the same geographical area (Bayle-Sempere et al. 2002). We also grouped fish species into the six spatial use categories defined by Harmelin (1987), constructed according to diet, home range and mobility. “Reduced” total abundance and biomass were also estimated by excluding from the calculations all species belonging to spatial categories 1 (comprising pelagic and erratic species), 2 (including shoaling species occupying the water column),

and those species belonging to category 6 that were particularly cryptic or hidden (conger-eel *Conger conger*, moray-eel *Muraena helena*, forkbeard *Phycis phycis* and scorpionfishes *Scorpaena* spp.), because they could not be accurately censused in a multi-species visual survey (Harmelin-Vivien et al. 1985, Thresher and Gunn 1986, Lincoln Smith 1989).

To quantify the multi-scale spatial variation in fish assemblages, data on fish abundance and biomass (total, by species and by spatial categories), species richness, diversity and habitat descriptors were analysed using mixed analysis of variance (Underwood 1997). Analyses were performed only on those non-pelagic taxa sufficiently present throughout the study, i.e. with a frequency of occurrence  $f \geq 15\%$ . To specifically test the hypothesis that observed abundance and biomass were higher within marine protected areas than in unprotected localities, a fixed factor Protection status ( $P$ ) was established. In order to attain a balanced design, data of Columbretes Natural Park were excluded from the analysis. In addition, since factors other than protection acting at a large geographical spatial scale could be confounding the results of analysis, data were analysed introducing also the fixed geographical factor Region ( $R$ ), by grouping one protected and the closer unprotected area (R1: Cabo de Gata–Aguilas; R2: Cabo de Palos–Isla Grosa; R3: Cabrera–western Mallorca). This regional factor is considered to be fixed, since it represents well known hydrographical latitudinal and island-to-continent differences. Firstly, primary production in the western Mediterranean increases from the Balearic Islands southwards and towards the continent, from  $< 100$  to  $> 300$  mg C m<sup>-2</sup> day<sup>-1</sup>, at least in autumn (Estrada 1981; Estrada et al. 1985). The nutrient enrichment in the southern basin is probably associated with the inflow of nutrient-rich Atlantic water through the Strait of Gibraltar, and the resulting circulation patterns, which include turbulent mixing in the Strait, upwelling in the Alborán Sea and the frontal zone of Almería-Oran (Estrada 1996). For its part, permanent frontal structures (Font et al. 1988), modified at small-scale and short-term by hydrographical instabilities, such as eddies and filaments (Millot 1987; Estrada 1996), in combination with river runoff (Lefèvre et al. 1997) and local upwelling created by submarine canyons (Masó et al. 1990; Alvarez et al. 1996), would be responsible for the coastal-island gradient. Secondly, a climatic gradient is in place in the western Mediterranean basin, as seawater temperature is warmer off the southern coasts than off the Catalan coast and the Gulf of Lyon (Tziperman and Malanotte-Rizzoli 1991; Crise et al. 1999). Finally, medium and small-scale “purely spatial” variation was introduced in the linear model as successively nested random factors Sectors ( $S$ ) and Zones ( $Z$ ). The resulting linear model, under the null hypothesis that each variable tested is homogeneous across the considered spatial factors and levels of protection, is then

$$X_{ijklm} = \mu + P_i + R_j + P_i \times R_j + S_k(P_i \times R_j) + Z_l(S_k(P_i \times R_j)) + T_{ijklm}$$

where  $X_{ijklm}$  is each individual value of the dependent variable,  $\mu$  is the overall mean,  $P_i$  is the effect of the  $i$ th level of protection (protected versus unprotected),  $R_j$  is the effect of the  $j$ th region,  $S_k(P_i \times R_j)$  is the effect of the  $k$ th sector,  $Z_l(S_k(P_i \times R_j))$  is the effect of the  $l$ th zone, and  $T_{ijklm}$  is the random error term (transects). If there were significant interaction between the regions  $R_j$  and the treatment  $P_i$ , further analyses were done as independent comparisons of protected versus unprotected areas in each region, by means of multiple comparisons using the Student–Newman–Keuls (SNK) procedure; otherwise, regional data were checked for pooling in order to improve the power of the analysis, provided that our experimental design was balanced (Underwood 1997). Prior to analyses, homogeneity of variances was checked using Cochran’s test, and heterogeneity was removed by transformation of the data to  $\log(x+1)$ ,  $(x+1)^{0.5}$  or combinations of both. In some cases, transformations did not remove heterogeneity, but we performed the analyses anyway, since analysis of variance is quite robust to departures from the underlying assumptions, especially when the design is balanced and contains a large number of samples or treatments (Underwood 1997). In these cases, test results have to be taken cautiously when the significance of the effect is  $0.01 < P < 0.05$ .

To explore the spatial variation of fish assemblages in relation to habitat structure, we performed a Principal Components Analysis (PCA), followed by its canonical counterpart Redundancy Analysis (RDA) (ter Braak and Prentice 1988) using both transformed abundance and biomass data, after giving a weight of 0 to those very abundant, highly mobile, pelagic species belonging to spatial category 1 of Harmelin (1987) that could distort the results. Results of ordination are displayed in a biplot, scaling the axes adjusting the species’ scores to the species’ variance: the resulting scores are correlations between species and eigenvectors. We evaluated the relative contribution of each variable to the ordination established by the RDA with a Monte Carlo permutation test after performing a forward selection of variables at the 0.1% level of significance. All these calculations were done using the CANOCO v. 3.15 package (ter Braak 1990). To explore the relationship between habitat variables (including their quadratic and cubic terms) and the values of fish abundance—total, by non-pelagic species sufficiently frequent ( $f \geq 15\%$  in the case of all data, or  $\geq 33\%$  at each locality) and by spatial categories—multiple regressions were performed using STATISTIX v. 4.0 package (Analytical Software 1992). Prior to regression analyses, the extreme and influential cases were detected (and subsequently removed) by carrying out analyses of residuals (McCullagh and Nelder 1989; Garcia-Charton and Pérez-Ruzafa 1998).

To quantify the spatial variation after extracting the variation due to the influence of habitat variables, residuals of regression analyses were used as dependent variables in the above four-factor, mixed analyses of variance (Grigg 1994; Chapman and Kramer 1999).

## Results

### Fish assemblage

We observed a total of 56 fish species (belonging to 21 families) during this study (Table 2), of which 22 species appeared in all localities (Table 3). Mean species richness was  $16 \pm 0.3$  (SEM, standard error of the mean) species 250-m<sup>-2</sup>, and mean total abundance was  $714 \pm 38.9$  (SEM) individuals 250-m<sup>-2</sup>. Total biomass averaged  $49,481 \pm 9,462.9$  (SEM) g 250-m<sup>-2</sup> ( $= 1,979.2$  kg ha<sup>-1</sup>). “Reduced” abundance and biomass—i.e. excluding from the summation pelagic (categories 1 and 2) and cryptic species—attained values of  $172 \pm 10.0$  (SEM) individuals and  $16,428 \pm 1,221.8$  (SEM) g 250-m<sup>-2</sup>, respectively. The value of the species diversity index  $H'_y$  (i.e. considering all transects together) was 2.86 bits per individual. Sparidae (13 species), Labridae (12 species) and Serranidae (8 species) were the families presenting the highest number of species. The 7 most frequent species ( $f \geq 70\%$ ; see Table 2) represented 67.5% of total abundance, but only 17.5% of total biomass. Another 10 species were frequent, while 12 species were common, and 27 species turned out to be occasional ( $f < 15\%$ ), since they appeared in fewer than 28 out of 189 transects (Table 2).

### Multi-scaled spatial pattern of fish assemblage and the effects of protection measures

The factor Protection ( $P$ ) turned out to be significant for species richness, total abundance and total biomass of

**Table 2** Mean values of total abundance (*ABUND*) (number of individuals) and biomass (*BIOM* in grams) per 250-m<sup>2</sup> ( $\pm$  standard error of the mean, SEM), percentage (% *FREQ*) and class (*FREQ*) of frequency of occurrence, and spatial category (*CAT*) of the fish

species observed in the present study. Abbreviations of species names used in Fig. 5 are also indicated (*O* occasional; *C* common; *F* frequent; *VF* very frequent)

Families	Species	Abbrev.	ABUND	$\pm$ SEM	BIOM	$\pm$ SEM	% FREQ	FREQ	CAT
Engraulidae	<i>Engraulis encrasicolus</i>	Engr	9.0	$\pm$ 5.0	9.6	$\pm$ 5.3	2.6	O	1
Muraenidae	<i>Muraena helena</i>	Mhel	0.4	$\pm$ 0.1	455.6	$\pm$ 94.2	24.3	C	6
Congridae	<i>Conger conger</i>	Cong	0.01	$\pm$ 0.01	4.2	$\pm$ 4.2	0.5	O	6
Gadidae	<i>Phycis phycis</i>	Phyc	0.02	$\pm$ 0.01	3.9	$\pm$ 2.8	1.6	O	6
Serranidae	<i>Anthias anthias</i>	Anth	12.6	$\pm$ 4.0	33.7	$\pm$ 9.9	10.1	O	2
	<i>Epinephelus costae</i>	Ecos	0.4	$\pm$ 0.1	228.4	$\pm$ 81.8	18.5	C	5
	<i>Epinephelus marginatus</i>	Emar	1.0	$\pm$ 0.1	2,091.5	$\pm$ 503.8	43.4	F	5
	<i>Epinephelus caninus</i>	Ecan	0.1	$\pm$ 0.02	33.0	$\pm$ 15.5	4.8	O	5
	<i>Mycteroperca rubra</i>	Mrub	0.1	$\pm$ 0.1	280.3	$\pm$ 246.9	1.6	O	5
	<i>Serranus atricauda</i>	Satr	0.1	$\pm$ 0.03	3.1	$\pm$ 1.5	3.2	O	5
	<i>Serranus cabrilla</i>	Scab	2.0	$\pm$ 0.2	63.4	$\pm$ 6.0	68.8	F	5
	<i>Serranus scriba</i>	Sscr	3.4	$\pm$ 0.2	135.0	$\pm$ 13.2	88.9	VF	5
Apogonidae	<i>Apogon imberbis</i>	Apog	16.0	$\pm$ 4.2	74.4	$\pm$ 18.7	68.8	F	6
Carangidae	<i>Seriola dumerilii</i>	Sdum	1.3	$\pm$ 0.5	3,434.8	$\pm$ 2,076.0	9.5	O	1
	<i>Trachurus mediterraneus</i>	Tmed	0.04	$\pm$ 0.04	9.1	$\pm$ 9.1	0.5	O	1
Coryphaenidae	<i>Coryphaena hippurus</i>	Chip	0.01	$\pm$ 0.01	4.6	$\pm$ 3.5	1.1	O	1
Haemulidae	<i>Parapristipoma octolineatum</i>	Poct	0.5	$\pm$ 0.3	120.9	$\pm$ 79.9	2.6	O	5
	<i>Pomadasys incisus</i>	Pinc	0.01	$\pm$ 0.01	0.1	$\pm$ 0.1	0.5	O	5
Sciaenidae	<i>Sciaena umbra</i>	Sumb	3.2	$\pm$ 0.8	639.9	$\pm$ 171.6	20.6	C	5
Mullidae	<i>Mullus surmuletus</i>	Mull	2.7	$\pm$ 0.6	141.6	$\pm$ 24.0	48.7	F	4
Sparidae	<i>Boops boops</i>	Boop	86.0	$\pm$ 16.5	582.7	$\pm$ 163.2	27.5	C	1
	<i>Dentex dentex</i>	Dent	3.6	$\pm$ 1.2	6.9	$\pm$ 3.8	18.0	C	3
	<i>Diplodus annularis</i>	Dann	3.0	$\pm$ 0.4	70.7	$\pm$ 11.2	54.5	F	3
	<i>Diplodus cervinus</i>	Dcer	0.1	$\pm$ 0.03	18.5	$\pm$ 6.8	7.4	O	3
	<i>Diplodus puntazzo</i>	Dpun	1.4	$\pm$ 0.3	155.8	$\pm$ 34.9	33.3	C	3
	<i>Diplodus sargus</i>	Dsar	5.0	$\pm$ 1.0	717.8	$\pm$ 211.0	58.2	F	3
	<i>Diplodus vulgaris</i>	Dvul	25.1	$\pm$ 3.9	1,737.5	$\pm$ 254.8	97.4	VF	3
	<i>Oblada melanura</i>	Obla	26.4	$\pm$ 5.5	1,680.2	$\pm$ 425.8	55.6	F	1
	<i>Pagellus acarne</i>	Page	0.2	$\pm$ 0.2	6.0	$\pm$ 6.0	0.5	O	3
	<i>Pagrus pagrus</i>	Pagr	0.2	$\pm$ 0.1	16.1	$\pm$ 6.8	4.2	O	3
	<i>Sarpa salpa</i>	Sarp	20.4	$\pm$ 2.5	2,669.0	$\pm$ 405.7	63.5	F	3
	<i>Sparus aurata</i>	Saur	0.2	$\pm$ 0.1	157.6	$\pm$ 67.8	6.9	O	3
	<i>Spondyliosoma cantharus</i>	Scan	1.3	$\pm$ 0.3	214.1	$\pm$ 54.6	27.5	C	3
Centracanthidae	<i>Spicara maena</i>	Smae	9.7	$\pm$ 5.0	342.9	$\pm$ 217.2	14.3	O	1
	<i>Spicara smaris</i>	Ssma	0.3	$\pm$ 0.2	3.9	$\pm$ 2.2	2.1	O	1
Pomacentridae	<i>Chromis chromis</i>	Chro	375.3	$\pm$ 25.5	1,021.9	$\pm$ 88.9	99.5	VF	2
Labridae	<i>Coris julis</i>	Cjul	32.7	$\pm$ 2.7	147.3	$\pm$ 9.7	98.9	VF	5
	<i>Labrus merula</i>	Lmer	0.2	$\pm$ 0.1	803.5	$\pm$ 263.6	16.4	C	5
	<i>Labrus viridis</i>	Lvir	0.1	$\pm$ 0.02	234.1	$\pm$ 72.8	7.9	O	5
	<i>Symphodus cinereus</i>	Scin	0.02	$\pm$ 0.02	0.1	$\pm$ 0.1	1.1	O	5
	<i>Symphodus doderleini</i>	Sdod	0.2	$\pm$ 0.04	2.0	$\pm$ 0.4	15.3	C	5
	<i>Symphodus mediterraneus</i>	Smed	1.5	$\pm$ 0.1	16.0	$\pm$ 1.5	58.7	F	5
	<i>Symphodus melanocercus</i>	Smel	0.4	$\pm$ 0.1	2.2	$\pm$ 0.4	29.6	C	5
	<i>Symphodus ocellatus</i>	Soce	6.5	$\pm$ 0.7	22.5	$\pm$ 2.3	74.6	VF	5
	<i>Symphodus roissali</i>	Sroi	0.7	$\pm$ 0.1	7.4	$\pm$ 0.9	37.0	C	5
	<i>Symphodus rostratus</i>	Sros	0.8	$\pm$ 0.1	8.0	$\pm$ 1.0	41.3	F	5
	<i>Symphodus tinca</i>	Stin	6.0	$\pm$ 0.4	548.3	$\pm$ 64.5	93.7	VF	5
	<i>Thalassoma pavo</i>	Thal	32.5	$\pm$ 4.4	108.0	$\pm$ 11.0	96.3	VF	5
Scombridae	<i>Sarda sarda</i>	Sard	0.2	$\pm$ 0.2	1,427.9	$\pm$ 1,413.0	1.1	O	1
Sphyraenidae	<i>Sphyraena</i> sp.	Sphy	14.3	$\pm$ 4.8	23,692.4	$\pm$ 8,433.7	22.2	C	1
Mugilidae	<i>Mugilidae</i> spp	Mugi	1.0	$\pm$ 0.2	310.0	$\pm$ 111.5	13.2	O	1
Scorpaenidae	<i>Scorpaena porcus</i>	Spor	0.1	$\pm$ 0.1	15.3	$\pm$ 15.3	0.5	O	6
	<i>Scorpaena notata</i>	Snot	0.01	$\pm$ 0.01	0.2	$\pm$ 0.2	1.1	O	6
	<i>Scorpaena scrofa</i>	Scor	0.01	$\pm$ 0.01	1.3	$\pm$ 1.3	0.5	O	6
Balistidae	<i>Balistes carolinensis</i>	Bali	0.01	$\pm$ 0.01	4.0	$\pm$ 2.8	1.1	O	1
Atherinidae	<i>Atherina hepsetus</i>	Athe	5.3	$\pm$ 3.7	7.2	$\pm$ 5.1	1.1	O	1

fish (Table 4), so that these variables usually attained higher average values per transect within marine protected areas (Fig. 2). Note that the significance of this factor was maintained despite the trend to slightly higher mean values of richness and abundance (but not of

biomass) for the whole locality in Aguilas compared to Cabo de Gata Natural Park. Only 7 species out of the 26 most frequent (i.e. presenting a frequency  $f \geq 15\%$ ), non-pelagic species analysed showed significantly different mean abundances between protected and unprotected

**Table 3** Number of species, diversity index,  $H'$ , mean values of fish assemblage parameters, and mean abundance per 250-m<sup>2</sup> ( $\pm$  standard error of the mean, SEM) of the fish species visually censused in the seven studied localities situated in the western Mediterranean Sea

	C. GATA	AGUILAS	C. PALOS	I. GROSA	CABRERA	MALLORCA	COLUMBRETES
Number of species	40	41	40	31	37	32	36
Species diversity index $H'$	2.8428	3.0605	2.5402	2.1911	2.6294	2.0989	2.3408
Mean sp. richness	15.7	17.3	14.2	11.9	19.3	15.6	18.1
Mean abundance	781.7	921.3	951.3	488.7	466.9	445.8	939.3
Mean biomass	71,430.0	28,290.0	109,700.0	10,210.0	23,960.0	7,224.7	9,5550.0
<i>E. encrasicolus</i>	2.1	23.8	-	37.0	±1,306.7	±10,390.0	-
<i>M. helena</i>	0.4	±0.15	0.8	±0.26	±0.04	±0.18	±0.11
<i>C. conger</i>	0.04	±0.04	0.04	-	-	-	-
<i>P. phycis</i>	0.04	±0.04	0.04	±0.04	-	-	-
<i>A. anthias</i>	-	18.7	65.1	±19.17	4.4	±2.98	-
<i>E. costae</i>	2.4	±0.52	0.1	±0.11	0.2	±0.08	-
<i>E. marginatus</i>	1.6	±0.46	0.6	±0.22	2.3	±0.28	±0.45
<i>E. caninus</i>	0.2	±0.11	0.1	±0.07	0.1	±0.05	-
<i>M. rubra</i>	-	0.04	±0.04	-	0.1	±0.04	±0.40
<i>S. atricauda</i>	0.3	±0.17	0.04	±0.04	-	-	-
<i>S. cabrilla</i>	3.8	±0.81	2.3	±0.33	2.4	±0.39	±0.24
<i>S. scriba</i>	6.0	±0.78	1.2	±0.23	3.0	±0.35	±0.31
<i>A. imberbis</i>	18.5	±11.44	8.2	±2.26	7.2	±1.68	±0.72
<i>S. dumerili</i>	0.04	±0.04	2.9	±1.31	0.04	±0.04	±2.99
<i>T. mediterraneus</i>	-	-	0.3	±0.29	-	-	-
<i>C. hippurus</i>	0.04	±0.04	0.04	±0.04	-	-	-
<i>P. octolineatum</i>	3.5	±2.28	0.3	±0.18	-	-	-
<i>P. incisus</i>	-	-	0.04	±0.04	-	-	-
<i>S. umbra</i>	1.7	±0.84	0.9	±0.69	0.4	±0.24	±4.46
<i>M. surmuletus</i>	8.9	±3.64	4.3	±0.24	2.1	±0.59	±0.35
<i>B. boops</i>	132.0	±51.30	86.4	±31.77	25.8	±18.24	±25.68
<i>D. dentex</i>	-	0.0	0.0	±0.05	0.1	±0.09	±7.39
<i>D. annularis</i>	0.2	±0.07	5.0	±1.47	7.8	±1.57	-
<i>D. cervinus</i>	0.3	±0.16	0.1	±0.10	0.9	±0.21	±0.04
<i>D. puntazzo</i>	0.6	±0.35	3.2	±2.10	3.4	±1.02	±0.32
<i>D. sargus</i>	2.0	±0.93	14.0	±3.53	2.6	±1.16	±0.36
<i>D. vulgaris</i>	43.7	±23.52	25.4	±4.61	14.3	±4.15	±9.36
<i>O. melanura</i>	37.0	±20.40	75.8	±25.72	4.6	±1.54	±6.98
<i>P. acarne</i>	-	1.7	±1.71	±13.29	6.7	±2.08	±20.6
<i>P. pagrus</i>	0.04	±0.04	0.04	±0.04	-	-	±0.05
<i>S. salpa</i>	9.7	±3.67	35.5	±10.86	4.4	±3.98	±4.37
<i>S. aurata</i>	-	-	0.04	±0.04	0.04	±0.04	±0.32
<i>S. cantharus</i>	-	-	0.1	±0.11	1.4	±0.34	±1.28
<i>S. maena</i>	-	53.0	±33.13	6.3	5.4	±2.57	±0.33
<i>S. smaris</i>	-	1.5	±1.42	-	-	-	±0.71
<i>C. chromis</i>	347.9	±61.15	527.7	±39.19	274.0	±54.10	±80.63
<i>C. julis</i>	70.7	±7.70	32.7	±7.55	23.5	±1.96	±1.85
<i>L. merula</i>	0.04	±0.04	0.04	±0.07	0.6	±0.13	±0.33
<i>L. viridis</i>	-	-	-	±0.04	0.3	±0.10	±0.10
<i>S. cinereus</i>	0.1	±0.11	-	-	-	-	-
<i>S. doderleini</i>	0.4	±0.11	0.5	±0.04	0.1	±0.07	±0.10
<i>S. mediterraneus</i>	0.7	±0.18	0.5	±0.23	2.1	±0.35	±0.41

<i>S. melanocercus</i>	0.04	±0.04	0.4	±0.14	-	0.2	±0.10	0.7	±0.14	1.1	±0.19	0.4	±0.13
<i>S. ocellatus</i>	9.1	±3.00	7.0	±2.21	2.6	4.7	±1.72	7.3	±1.82	3.3	±0.56	11.5	±1.41
<i>S. roissali</i>	0.8	±0.21	0.6	±0.15	0.4	0.5	±0.14	0.9	±0.33	0.7	±0.27	0.9	±0.28
<i>S. rostratus</i>	1.6	±0.28	1.1	±0.24	0.1	0.3	±0.11	0.6	±0.17	1.4	±0.37	0.1	±0.06
<i>S. tinca</i>	10.6	±1.62	9.0	±1.47	2.6	5.8	±1.05	4.3	±0.67	5.3	±0.55	4.4	±0.48
<i>T. pavo</i>	32.2	±4.15	22.0	±3.30	99.1	40.6	±4.90	10.9	±1.40	6.6	±0.97	16.1	±2.49
<i>S. sarda</i>	-	-	-	-	-	-	-	-	-	-	-	1.6	±1.42
<i>Sphyracnasp.</i>	31.9	±21.11	-	-	40.3	0.3	±0.29	15.7	±11.67	0.3	±0.29	11.9	±3.62
<i>Mugilidae spp.</i>	0.4	±0.31	0.7	±0.65	0.9	0.3	±0.29	1.4	±0.81	0.4	±0.31	2.6	±0.99
<i>S. porcus</i>	-	-	-	-	0.7	-	-	-	-	-	-	-	-
<i>S. notata</i>	0.04	±0.04	-	-	-	-	-	0.04	±0.04	-	-	-	-
<i>S. serofo</i>	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>B. carolinensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>A. hepsetus</i>	-	-	-	-	37.0	-	-	-	-	-	-	-	-

areas that were consistent among regions (Table 4), of which 5 commercial (*Sciaena umbra*, *Diplodus annularis*, *D. sargus*, *D. vulgaris*, and *Sarpa salpa*) and one non-commercial (*Apogon imberbis*) species were in general more abundant within marine reserves (Fig. 3). Again the significance of this factor was maintained even though mean abundances were generally higher in Aguilas than in Cabo de Gata. Only one non-target species (*Symphodus rostratus*) showed a trend to higher abundance in control areas not subject to fishing. Spatial categories 3 (comprising mainly sparids) and 6 (cryptic, sedentary, mostly non-target species) showed higher abundance within protected areas, regardless of the region considered (Table 4). Several species, as blacktail comber (*Serranus atricauda*), bastard grunt (*Pomadasy incisus*) and gilt-head sea bream (*Sparus aurata*), were observed only within protected areas, whereas other species (e.g. *Epinephelus caninus*, *Diplodus cervinus*, *Thalassoma pavo*) showed a non-significant trend to greater abundance inside protected areas.

The factor Region had an additional significant effect on average values of total abundance, total biomass and species richness per transect (Table 4; Fig. 2). Region 3 (comprising Cabrera National Park and unprotected sites in western Mallorca, located in the northern part of the study area) harboured lower average abundance and biomass than the other two regions. For its part, mean species richness was lower in region 2 (Cabo de Palos Marine Reserve and Isla Grosa) than elsewhere, while Shannon's species diversity index,  $H'$ , was significantly higher for the southernmost region 1 (Cabo de Gata Marine Park and Aguilas) than for the other two regions. Twelve species out of 26 exhibited significant differences in average abundance among regions (Table 4). For the "ubiquitous" species, variation in density amongst localities ranged from 4- to 5-fold for *Serranus scriba*, *Coris julis* and *Symphodus tinca* to about 500-fold for *Sciaena umbra*. The difference was 14- to 40-fold for the other species (Table 3). Generally, the southernmost regions 1 and 2 harboured the highest values of mean abundance per species, the only exceptions being the cases of annular sea bream (*Diplodus annularis*), black sea bream (*Spondyliosoma cantharus*) and blacktail wrasse (*Symphodus melanocercus*), which showed instead a north-to-south decrease of abundance (Tables 3, 4; Fig. 3). Also, categories 4, 5 (comprising mainly serranids and labrids) and 6 exhibited significant differences among regions, so that, for the three categories, region 1 (Cabo de Gata Natural Park and Aguilas unprotected sites) was the one with the higher values (Table 3). Other occasional species were observed only in a few localities, such as *Serranus atricauda*, *Parapristipoma octolineatum* (these two species being present only in the three southernmost localities) and *Mycteroperca rubra*, which was only observed in Aguilas and Columbretes (Table 3).

Five species out of 26 showed a significant interaction between factors Region and Protection (Table 4).

**Table 4** Results of mixed analysis of variance showing the effects across the western Mediterranean Sea of the factors Region (R), Protection status (P) and their interaction (R×P), Sector (S) and Zone (Z) on fish assemblage descriptors, on the abundance and biomass of the 26 most frequent, non-pelagic species, and on the spatial categories of Harmelin (1987), indicating the factors at which significant variation exists (ns not significant; \* P<0.05; \*\*P<0.01; \*\*\* P<0.001). If significance of factors for any variables changes using biomass instead of abundance data, the new

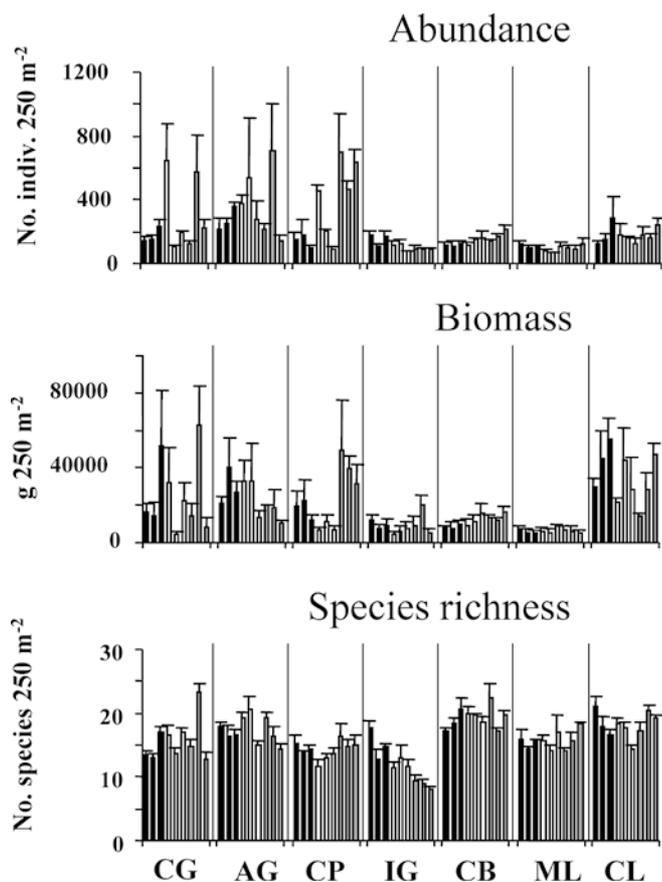
level of significance is indicated after the sign “/”. Results of Cochran’s and Student–Newman–Keuls (SNK) tests are also shown; in the latter case, Regions (R) have three levels (1,2 and 3) whose numbering corresponds to that indicated in the text, and Protection levels (P) have two levels (1 protected, and 2 unprotected). The last columns, under the heading “Residuals of abundance”, indicate the result of the same analysis performed on the data corrected for the effect of habitat structure by using residuals of multiple regression analyses as dependent variables (see text for further explanation)

	Abundance/biomass					SNK results	Cochran’s test	Residuals of abundance				
	R	P	R×P	S(R×P)	Z(S (R×P))			R	P	R×P	S(R×P)	Z(S (R×P))
Total abundance	*	*	ns	*	***	R: 1=2>3; P: 1>2	ns	**	*	ns	ns	**
Total biomass	*	*	ns	ns	*	R: 1=2>3; P: 1>2	*	*	*	ns	ns	ns
Species richness	***	**	ns	ns	***	R: 2<1=3; P: 1>2	ns	*	*	ns	ns	***
Diversity index H'	*	ns	ns	ns	ns	R: 1>2=3	ns	ns	ns	ns	ns	ns
<i>M. helena</i>	ns	ns	ns	*	*/ns	–	ns	ns	ns	ns	ns	*
<i>E. costae</i>	***/ns	***/ns	***/ns	ns	*/ns	P: R1:1>2; R2:1>2	ns/**	***	*	***	ns	ns
<i>E. marginatus</i>	***/ns	***/ns	***/*	ns/*	*/ns	R: 1=3>2; P: 1>2	*/ns	**	*	**	ns	ns
<i>S. cabrilla</i>	ns	ns	*/ns	**/ns	ns	P: R1:1>2	ns	ns	ns	ns	ns	ns
<i>S. scriba</i>	**/**	ns	ns	*/ns	ns	R: 1>2=3	ns	*	ns	ns	ns	ns
<i>A. imberbis</i>	**/*	**/ns	ns	ns/*	*/ns	R: 1>2>3; P: 1<2 / R: ns	ns	*	*	ns	ns	*
<i>S. umbra</i>	*/ns	*/ns	ns	ns	***/*	R: 1>2=3	**	ns	ns	ns	ns	**
<i>M. surmuletus</i>	*/**	ns	ns	***/*	ns	R: 1>2=3	ns	–	–	–	–	–
<i>D. dentex</i>	ns	ns	ns	**/*	***	–	**	ns	ns	ns	ns	**
<i>D. annularis</i>	**	*/ns	ns	**	**/ns	R: 1=2<3; P: 1>2	ns	*	ns	ns	*	*
<i>D. puntazzo</i>	ns	ns/*	ns	**	ns/*	/ P: 1>2	**/ns	ns	ns	ns	*	ns
<i>D. sargus</i>	ns	**	ns	ns/**	***/*	P: 1>2	ns	ns	*	ns	ns	**
<i>D. vulgaris</i>	ns	*	ns	ns	***	P: 1>2	ns	ns	ns	ns	ns	***
<i>S. salpa</i>	ns	**/*	ns	***	ns	P: 1>2	ns	ns	ns	ns	***	ns
<i>S. cantharus</i>	***	ns	ns	ns	ns/*	R: 1=2<3	*/ns	*	ns	ns	ns	*
<i>C. chromis</i>	ns	ns	ns	**/**	*/ns	–	**/ns	ns	ns	ns	**	ns
<i>C. julis</i>	***/ns	ns	**/ns	ns/**	***/*	R: 1>2>3	*/**	**	ns	ns	ns	**
<i>L. merula</i>	ns	ns	*	**/*	ns	P: R3:1>2	*/ns	*	ns	*	ns	*
<i>S. doderleini</i>	***	ns	ns	ns	ns	R: 1>2=3	*/ns	**	ns	ns	ns	ns
<i>S. mediterraneus</i>	***	ns	ns	ns	***/*	R: 2<1<3	ns	**	ns	ns	ns	***
<i>S. melanorcercus</i>	***/*	ns	ns/*	*/ns	ns	R: 1=2<3	ns	**	ns	ns	*	ns
<i>S. ocellatus</i>	ns	ns	ns	***	ns	–	ns	ns	ns	ns	**	ns
<i>S. roissali</i>	ns	ns	ns	*/ns	ns/**	–	ns	ns	ns	ns	*	ns
<i>S. rostratus</i>	***	*/ns	ns	ns	ns	R: 1>3>2; P: 1<2	ns	**	*	ns	ns	ns
<i>S. tinca</i>	*/**	ns	ns	*/ns	ns	R: 1>2=3	ns/**	*	ns	ns	ns	ns
<i>T. pavo</i>	***/ns	ns	ns	*/**	**/ns	R: 2>1>3	ns/**	***	ns	ns	ns	ns
Category 1	ns	ns	ns	*	***	–	**	ns	ns	ns	ns	***
Category 2 §	ns	ns	ns	***	ns	–	**	ns	ns	ns	***	ns
Category 3	ns	**	ns	*	***	P: 1>2	ns	ns	ns	ns	*	***
Category 4	*	ns	ns	***	ns	R: 1>2=3	ns	–	–	–	–	–
Category 5	***	ns	***	ns	**	R: 1=2>3	ns	***	ns	***	ns	**
Category 6	*	**	ns	ns	*	R: 1>2=3; P: 1<2	ns	*	**	ns	ns	**

Golden groupers (*Epinephelus costae*) were more abundant within than outside Cabo de Gata National Park, and were present in Cabrera but not in its control site at Mallorca; however, they had a similar abundance in Cabo de Palos marine reserve and in Isla Grosa (Table 3; Fig. 3). Analogously, dusky groupers (*E. marginatus*) were usually more abundant at the protected sites, except at Cabo de Palos, where the abundance of this species was not significantly different from that of its unprotected counterpart (Fig. 3). Combers (*Serranus cabrilla*) were more abundant inside reserves, but this effect was greater in region 1. For rainbow wrasses (*Coris julis*), the SNK test was not able to find which mean values were significantly different, although inspection of data indicated that again the difference between Cabo de Gata and Aguilas is much higher than

in the other two regions. Brown wrasses (*Labrus merula*) were only significantly more abundant within the Cabrera National Park compared to sites at Mallorca, and were not observed in Aguilas, but were observed in Cabo de Gata (Table 3).

In addition, all assemblage variables (except species diversity), all species (except *Symphodus doderleini* and *S. rostratus*) and all spatial categories exhibited significant spatial heterogeneity among sectors and/or zones, thus evidencing spatial heterogeneity at medium and/or small scale (Table 4). In all, 15 species showed significant heterogeneity among sectors separated by 1,000s of metres, and 13 species were spatially variable at the zone scale, i.e. among sites separated by 100s of metres. Among them, 5 species (*Muraena helena*, *Dentex dentex*, *Diplodus annularis*, *Chromis chromis* and *Thalassoma*



**Fig. 2** Mean values per 250-m<sup>2</sup> ( $\pm$  SEM,  $n=3$ ) of “reduced” abundance (*top panel*) and biomass (*middle panel*), and species richness (*bottom panel*) in each zone within each sector of each locality in the western Mediterranean Sea (CG Cabo de Gata, AG Aguilas, CP Cabo de Palos, IG Isla Grosa, CB Cabrera, ML Mallorca, CL Columbretes). Different grey levels of bars separate groups of zones within each sector at each locality

*pavo*) showed such a spatial variability at both medium and small scale.

Testing for the different factors considered using the values of biomass instead of abundance (see Table 5) gives slightly different results. Only four species showed a significant effect of protection status (Table 4). These differences are due to the fact that five species lose the significant effect of protection, and one (*Diplodus puntazzo*) showed significantly higher biomass within protected sites, but did not show such a difference in terms of abundance. Nine species showed different biomass among regions, so that three species lose the significance of this large-scale spatial factor compared to abundance data. And only three species showed a significant Protection  $\times$  Region interaction regarding biomass, owing to the loss of significance for two species compared to abundance values (Table 4). Those species’ biomasses for which factors Region or Protection remain still significant generally maintain the same trend as for abundance values. Ten species changed the significance of the differences among sectors, and 15 species did the same among zones, so that 10 species did not exhibit any

spatial heterogeneity at medium and/or small scale in terms of biomass.

#### Spatial variation in habitat structure

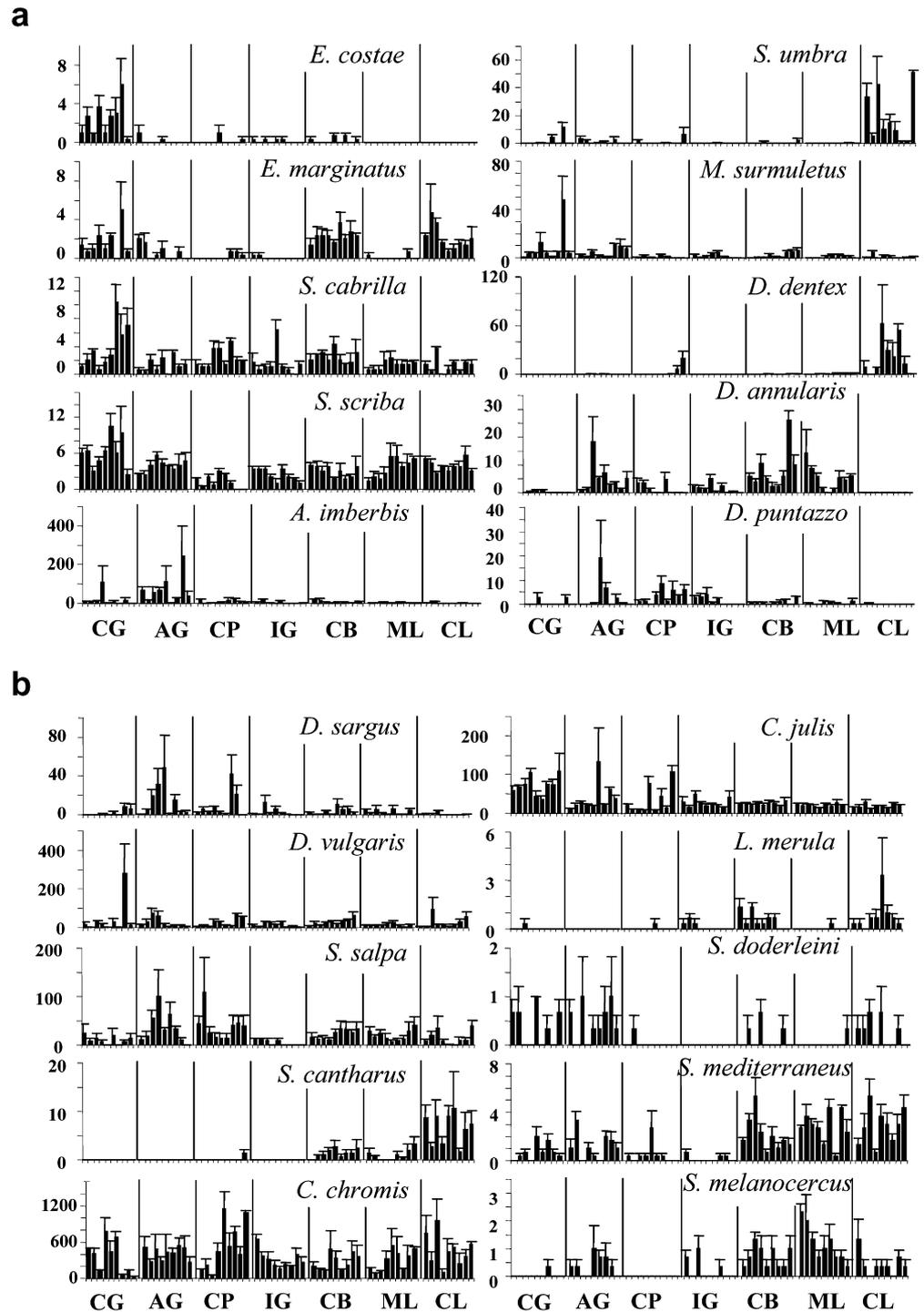
Table 6 shows the mean values and range of environmental variables used as descriptors of rocky reef habitat structure. It must be noted that *Posidonia oceanica* meadows were absent in Columbretes. Also, mean depth was 11.6 m, but ranged from 4 to 19 m, owing to the irregularity of the bottom topography in a few transects. No significant differences in habitat structure were detected among regions or protection levels, except in the case of verticality, in the sense that this habitat descriptor tended to attain higher average values within the transects performed at the northernmost region 3. On the other hand, small- and/or medium-scale spatial variability appeared to be significant for all environmental variables considered (Table 6).

#### The influence of rocky habitat structure on the fish assemblage

Eighteen percent of total variation in species richness was explained by the variation in maximum depth and number of medium-sized boulders (Table 7; Fig. 4a). The regression model constructed on the observed values of total abundance (after removing species belonging to spatial categories 1 and 2) incorporated five environmental variables to explain 21% of the variation. Abundance was generally higher in those transects situated on purely rocky, highly complex bottoms. The multiple regression analysis of total biomass and species diversity index,  $H'$ , accounted for only 9% and 3% of the variation of their estimated values, respectively. When we performed these analyses by localities for all four variables describing assemblage structure, we found that, generally, regression models were not consistent among localities. It was not possible to obtain a significant model for all localities, although when the model was significant, the proportion of variance explained was generally higher than in the case of the global analysis using all data together (Table 7). For instance, number of species responded to variations in the number of medium-sized boulders in Cabo de Palos (31%) (Fig. 4b) and Cabrera (33%), and to the proportion of sand cover in Isla Grosa (48%), whereas no significant models were obtained in the cases of Águilas, Cabo de Gata, Mallorca and Columbretes.

When exploring the relationship between abundance of the 26 most frequent non-pelagic species and their habitat (Table 8), we found that, except 4 species, all species showed significant models, but only for 10 species did the proportion of variance explained exceed 10%. Usually, species’ abundances responded—positively, negatively or non-linearly—to variations in the number of rocky boulders of different size, rock cover,

**Fig. 3** Mean abundance per 250-m<sup>2</sup> ( $\pm$  SEM,  $n=3$ ) of the most frequent fish species in each zone within each sector of each locality in the western Mediterranean Sea (see Fig. 2 for the abbreviations of localities). Y-axis scales differ among species



depth, or their combinations, while only one species (*Symphodus doderleini*) seemed to respond to variations in percentage cover by *Posidonia oceanica*. When we grouped species into spatial categories, for all categories (except category 4) we found significant regression models. These models accounted for 13–22% of total variation, except category 1 (pelagic species), whose model accounted, as expected, for only 3% of observed abundance (Table 8).

Significant models were found for 40–87% of the species analysed by locality. Generally the models differed depending on the locality. In the case of *Serranus cabrilla*, for example, minimum depth explained 16% of the variance in Cabo de Gata and 30% in Mallorca; rock cover explained 14% in Águilas; number of medium-sized boulders, 21% in Isla Grosa. Number of medium-sized boulders combined with rock cover explained 37% of variance in Cabo de Palos, and with

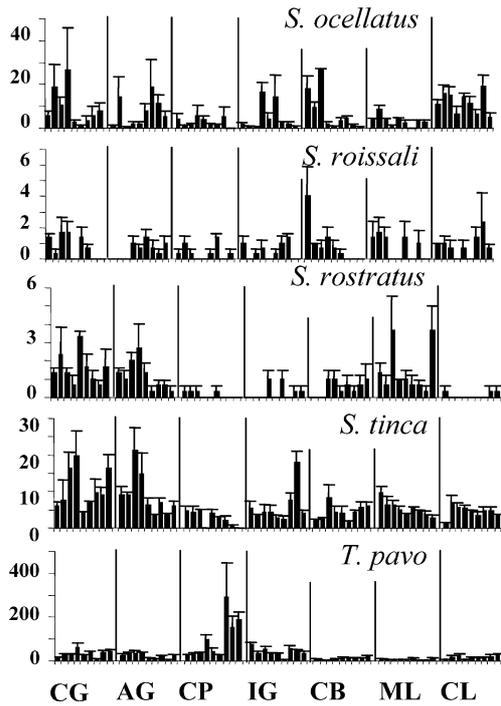


Fig. 3 (Contd.)

mean depth, 37% in Columbretes. Again the same pattern of high variability could be seen in the case of the species grouped by spatial categories (Table 8).

After the pelagic species were found to be passive in the analysis, axes 1 and 2 of PCA cumulatively accounted for 31% of total variance in the data, while axes 1–4 (which were found to be significant after a permutation test) accounted for 50% of total variation. In contrast, the first two axes of RDA performed on the fish abundance data accounted for only 8% of total variance in the data although relative positions of species and sites in the ordination diagram remain essentially unchanged between both analyses (Fig. 5a, b). The stepwise forward selection of habitat descriptors retained seven variables as having a significant influence on the assemblage structure (rock and *Posidonia* cover, number of small, medium-sized and large boulders, mean depth and verticality), these variables accounting for 13% of total variation (i.e. the inertia explained by the first four axes). Regarding habitat descriptors, the first axis seems to distinguish between purely rocky transects in its negative part, versus heterogeneous rocky bottoms (i.e. interspersed with sandy patches and clumps of *Posidonia*) in its positive region (Fig. 5a). The exclusively rocky transects were more frequent in Columbretes (where *Posidonia oceanica* is absent) and Cabo de Palos, and also in some sites in Cabo de Gata and Cabrera (all protected localities). Thereby, transects performed in these localities are located in the negative part of axis 1, which is associated with species such as *Anthias anthias*, *Spondylisoma cantharus*, *Dentex dentex*, *Sphyræna* sp., *Sciaena umbra*, *Diplodus vulgaris*,

*D. puntazzo*, *Muraena helena*, *Symphodus mediterraneus*, *Epinephelus marginatus* and *Chromis chromis*. The other localities (mostly those not protected) and some transects in Cabo de Gata and Cabrera harboured more heterogeneous bottoms, and species such as *Diplodus annularis*, *Symphodus rostratus*, other *Symphodus* spp., *Coris julis*, *Pagellus acarne*, *Pomadasyss incisus* or *Epinephelus costae* appeared to be related mostly to this part of the axis (Fig. 5a). A confounding effect of habitat structure and level of protection could be operating, as most sampling units performed within marine reserves are located in the negative part of axis 1 in RDA, while transects censused within non-protected areas are situated mostly in the positive part of this axis (Fig. 5b, c). Therefore, it would seem as if protected areas generally were situated over predominantly rocky, complex bottoms. Axis 2 seems to distinguish between rocky bottoms with a major proportion of large boulders (i.e., with large vertical walls dominating the seascape) in the negative part, with species such as *Sparus aurata*, *Myxeroperca rubra*, *Spondylisoma cantharus* or *Serranus cabrilla*. In the positive range, rocky substrates harboured a smaller-scale complexity (as determined by the number of small and medium-sized boulders), with *Apogon imberbis*, *Sarpa salpa*, *Diplodus sargus*, *Symphodus rostratus* or *Epinephelus caninus*, among other species (Fig. 5a).

In the case of RDA performed on the biomass data, the resulting ordination is similar to that determined by abundance data, since it explained only a small portion (8%) of total variance. In addition, the environmental variables selected by Monte Carlo procedure are the same, and the position of species, variables and sampling units remain essentially identical.

#### Interference of habitat structure on the effect of protection

To try to distinguish between effects of habitat and protection, we repeated the analysis of variance using the values of original variables after correcting for the effect of habitat by using residuals of multiple regression analyses as dependent variables. By doing so, we found some changes compared with the analyses performed on raw data (Table 4). Thereby, corrected values of total abundance and biomass, as well as the abundance of ten species have lost the significance of differences among sectors and/or zones, while two species (*Spondylisoma cantharus* and *Labrus merula*) gained significance of variability at small spatial scale (i.e. among zones separated by 100s of metres). On the other hand, four species (*Sciaena umbra*, *Diplodus annularis*, *D. vulgaris* and *Sarpa salpa*) and spatial category 3, previously found to show significant differences in abundance between protected and non-protected areas, lose this difference when we used abundance data corrected for the effect of habitat. In addition, corrected species diversity and abundance of

**Table 5** Mean biomass (in grams) per 250-m<sup>2</sup> ( $\pm$  standard error of the mean, SEM) of the fish species visually censused in the seven studied localities in the western Mediterranean Sea

	C. GATA		AGUILAS		C. PALOS		I. GROSA		CABRERA		MALLORCA		COLUMBRETES	
<i>E. encrasicolus</i>	6.8	$\pm$ 5.0	9.7	$\pm$ 9.7	–	–	50.6	$\pm$ 35.1	–	–	–	–	–	–
<i>M. helena</i>	569.8	$\pm$ 281.8	365.9	$\pm$ 166.0	1,024.6	$\pm$ 496.5	24.3	$\pm$ 24.3	495.8	$\pm$ 173.2	307.2	$\pm$ 108.4	401.7	$\pm$ 177.4
<i>C. conger</i>	29.5	$\pm$ 29.5	–	–	–	–	–	–	–	–	–	–	–	–
<i>P. phycis</i>	18.6	$\pm$ 18.6	1.9	$\pm$ 1.9	6.6	$\pm$ 6.6	–	–	–	–	–	–	–	–
<i>A. anthias</i>	–	–	33.9	$\pm$ 28.8	189.4	$\pm$ 54.5	–	–	12.8	$\pm$ 8.5	–	–	–	–
<i>E. costae</i>	1,005.9	$\pm$ 509.8	71.6	$\pm$ 54.7	255.7	$\pm$ 181.7	47.7	$\pm$ 28.9	217.9	$\pm$ 112.3	–	–	–	–
<i>E. marginatus</i>	1,552.0	$\pm$ 933.0	801.3	$\pm$ 324.7	624.6	$\pm$ 574.5	111.8	$\pm$ 100.6	1,087.4	$\pm$ 271.7	13.4	$\pm$ 7.9	10,450.0	$\pm$ 2,873.5
<i>E. caninus</i>	137.4	$\pm$ 93.8	72.2	$\pm$ 50.5	–	–	–	–	16.7	$\pm$ 14.5	4.8	$\pm$ 4.8	–	–
<i>M. rubra</i>	–	–	100.4	$\pm$ 100.4	–	–	–	–	–	–	–	–	1,861.5	$\pm$ 1,721.2
<i>S. atricauda</i>	17.5	$\pm$ 9.1	–	–	4.4	$\pm$ 4.4	–	–	–	–	–	–	–	–
<i>S. cabrilla</i>	137.4	$\pm$ 26.0	53.8	$\pm$ 11.6	75.4	$\pm$ 13.0	36.7	$\pm$ 12.7	67.7	$\pm$ 13.3	34.2	$\pm$ 9.4	38.8	$\pm$ 9.5
<i>S. scriba</i>	376.9	$\pm$ 70.3	148.9	$\pm$ 16.1	45.2	$\pm$ 9.3	65.1	$\pm$ 7.7	68.4	$\pm$ 8.0	87.2	$\pm$ 12.9	153.5	$\pm$ 14.7
<i>A. imberbis</i>	49.0	$\pm$ 13.0	333.3	$\pm$ 118.9	39.1	$\pm$ 10.2	25.9	$\pm$ 9.2	38.1	$\pm$ 9.2	24.1	$\pm$ 3.6	11.7	$\pm$ 5.5
<i>S. dumerilii</i>	26.9	$\pm$ 26.9	920.8	$\pm$ 436.6	–	–	–	–	15.8	$\pm$ 15.8	–	–	23,080.0	$\pm$ 14,160.0
<i>T. mediterraneus</i>	–	–	–	–	63.5	$\pm$ 63.5	–	–	–	–	–	–	–	–
<i>C. hippurus</i>	9.6	$\pm$ 9.6	0.1	$\pm$ 0.1	22.5	$\pm$ 22.5	–	–	–	–	–	–	–	–
<i>P. octolineatum</i>	829.9	$\pm$ 548.3	16.2	$\pm$ 11.4	–	–	–	–	–	–	–	–	–	–
<i>P. incisus</i>	–	–	–	–	0.6	$\pm$ 0.6	–	–	–	–	–	–	–	–
<i>S. umbra</i>	283.7	$\pm$ 144.0	82.7	$\pm$ 42.0	121.6	$\pm$ 97.9	1.0	$\pm$ 1.0	37.9	$\pm$ 25.1	2.9	$\pm$ 2.9	3,949.4	$\pm$ 982.0
<i>M. surmuletus</i>	406.8	$\pm$ 130.7	247.5	$\pm$ 60.6	18.3	$\pm$ 11.4	39.2	$\pm$ 12.7	146.3	$\pm$ 40.7	51.0	$\pm$ 16.9	82.3	$\pm$ 39.5
<i>B. boops</i>	1,269.1	$\pm$ 482.6	244.5	$\pm$ 84.3	902.1	$\pm$ 902.1	24.6	$\pm$ 17.6	98.1	$\pm$ 57.2	53.8	$\pm$ 27.5	1,486.7	$\pm$ 448.3
<i>D. dentex</i>	–	–	–	–	1.7	$\pm$ 1.2	–	–	0.01	$\pm$ 0.01	0.1	$\pm$ 0.1	46.2	$\pm$ 26.0
<i>D. annularis</i>	6.0	$\pm$ 2.8	197.6	$\pm$ 63.1	36.3	$\pm$ 12.0	35.1	$\pm$ 9.3	150.1	$\pm$ 25.7	69.8	$\pm$ 11.4	–	–
<i>D. cervinus</i>	31.6	$\pm$ 14.1	7.8	$\pm$ 4.3	89.9	$\pm$ 43.4	–	–	–	–	–	–	–	–
<i>D. puntazzo</i>	84.5	$\pm$ 47.6	268.0	$\pm$ 174.6	543.9	$\pm$ 138.1	44.0	$\pm$ 14.2	120.7	$\pm$ 31.1	24.5	$\pm$ 12.8	5.3	$\pm$ 5.3
<i>D. sargus</i>	272.0	$\pm$ 142.0	1,794.5	$\pm$ 749.9	2,040.9	$\pm$ 1213.6	88.2	$\pm$ 37.4	575.4	$\pm$ 172.1	129.6	$\pm$ 35.3	124.0	$\pm$ 55.4
<i>D. vulgaris</i>	2,920.2	$\pm$ 1,392.3	1,968.2	$\pm$ 582.8	1,754.0	$\pm$ 390.2	676.5	$\pm$ 136.2	1,565.4	$\pm$ 289.9	685.6	$\pm$ 223.8	2,592.8	$\pm$ 729.4
<i>O. melanura</i>	1,309.1	$\pm$ 560.6	5,144.4	$\pm$ 2,247.4	2,895.1	$\pm$ 1,540.4	178.2	$\pm$ 86.5	317.4	$\pm$ 106.6	122.6	$\pm$ 44.8	1,794.8	$\pm$ 801.3
<i>P. acarne</i>	–	–	42.1	$\pm$ 42.1	–	–	–	–	–	–	–	–	–	–
<i>P. pagrus</i>	1.4	$\pm$ 1.4	50.1	$\pm$ 29.2	23.6	$\pm$ 23.6	3.5	$\pm$ 3.5	–	–	–	–	33.8	$\pm$ 29.0
<i>S. salpa</i>	1,575.3	$\pm$ 674.7	3,371.3	$\pm$ 1,014.6	7,705.5	$\pm$ 2,084.4	427.2	$\pm$ 137.0	1,748.2	$\pm$ 358.9	1,663.7	$\pm$ 455.7	2,191.7	$\pm$ 912.8
<i>S. aurata</i>	–	–	–	–	103.9	$\pm$ 103.9	–	–	10.1	$\pm$ 10.1	–	–	989.4	$\pm$ 436.1
<i>S. cantharus</i>	–	–	–	–	26.2	$\pm$ 18.2	–	–	105.8	$\pm$ 33.4	19.5	$\pm$ 7.6	1,347.1	$\pm$ 302.6
<i>S. maena</i>	–	–	2,160.7	$\pm$ 1,493.5	–	–	143.5	$\pm$ 68.8	58.7	$\pm$ 55.5	31.2	$\pm$ 27.7	6.2	$\pm$ 6.2
<i>S. smaris</i>	–	–	9.9	$\pm$ 9.7	–	–	–	–	–	–	–	–	17.3	$\pm$ 12.0
<i>C. chromis</i>	1,496.2	$\pm$ 353.0	890.0	$\pm$ 199.4	1,168.3	$\pm$ 167.0	725.6	$\pm$ 100.9	608.0	$\pm$ 83.5	676.2	$\pm$ 99.9	1,588.9	$\pm$ 379.3
<i>C. julis</i>	320.9	$\pm$ 48.9	117.9	$\pm$ 10.9	103.6	$\pm$ 16.0	105.6	$\pm$ 10.5	135.1	$\pm$ 11.4	126.3	$\pm$ 14.5	121.4	$\pm$ 12.8
<i>L. merula</i>	330.0	$\pm$ 330.0	–	–	200.9	$\pm$ 200.9	431.9	$\pm$ 212.0	1,156.3	$\pm$ 300.7	137.0	$\pm$ 137.0	3,368.1	$\pm$ 1,698.9
<i>L. viridis</i>	–	–	–	–	–	–	4.8	$\pm$ 4.8	601.5	$\pm$ 215.5	239.2	$\pm$ 239.2	793.5	$\pm$ 373.2
<i>S. cinereus</i>	0.8	$\pm$ 0.7	–	–	–	–	–	–	–	–	–	–	–	–
<i>S. doderleini</i>	4.9	$\pm$ 1.5	5.7	$\pm$ 2.1	0.2	$\pm$ 0.2	–	–	1.6	$\pm$ 1.0	0.2	$\pm$ 0.2	1.6	$\pm$ 0.7
<i>S. mediterraneus</i>	11.0	$\pm$ 3.0	15.5	$\pm$ 4.3	5.4	$\pm$ 2.1	1.8	$\pm$ 1.1	23.8	$\pm$ 3.6	32.2	$\pm$ 4.7	22.6	$\pm$ 4.2
<i>S. melanorcercus</i>	0.4	$\pm$ 0.4	3.9	$\pm$ 1.5	–	–	1.6	$\pm$ 0.7	2.8	$\pm$ 0.8	4.2	$\pm$ 0.9	2.8	$\pm$ 1.1
<i>S. ocellatus</i>	32.1	$\pm$ 9.8	13.7	$\pm$ 2.8	6.1	$\pm$ 2.7	18.0	$\pm$ 5.1	34.1	$\pm$ 7.7	17.9	$\pm$ 3.6	35.8	$\pm$ 5.3
<i>S. roissali</i>	11.3	$\pm$ 3.3	7.1	$\pm$ 2.2	4.1	$\pm$ 1.5	6.2	$\pm$ 1.8	6.5	$\pm$ 2.1	9.5	$\pm$ 3.8	6.9	$\pm$ 2.1
<i>S. rostratus</i>	19.1	$\pm$ 4.2	16.3	$\pm$ 3.4	1.4	$\pm$ 0.7	2.9	$\pm$ 1.1	5.8	$\pm$ 2.0	9.9	$\pm$ 2.5	0.8	$\pm$ 0.5
<i>S. tinca</i>	1,245.0	$\pm$ 374.7	846.3	$\pm$ 96.4	340.9	$\pm$ 81.5	645.3	$\pm$ 130.7	234.0	$\pm$ 30.2	232.9	$\pm$ 29.6	294.1	$\pm$ 33.6
<i>T. pavo</i>	133.0	$\pm$ 17.0	85.2	$\pm$ 12.8	286.7	$\pm$ 58.7	103.4	$\pm$ 15.3	42.5	$\pm$ 5.4	35.0	$\pm$ 10.4	70.3	$\pm$ 10.4
<i>S. sarda</i>	–	–	–	–	–	–	–	–	–	–	–	–	9,995.0	$\pm$ 9,887.4
<i>S. sphyraena</i>	43,550.0	$\pm$ 29,630.0	–	–	85,590.0	$\pm$ 48,220.0	256.1	$\pm$ 256.1	11,710.0	$\pm$ 10,110.0	120.9	$\pm$ 101.4	24,620.0	$\pm$ 7,912.8
<i>Mugilidae</i> spp.	145.0	$\pm$ 123.3	113.0	$\pm$ 113.0	102.5	$\pm$ 66.8	74.2	$\pm$ 74.2	337.3	$\pm$ 249.8	82.0	$\pm$ 56.4	1315.8	$\pm$ 691.8
<i>S. porcus</i>	–	–	–	–	106.8	$\pm$ 106.8	–	–	–	–	–	–	–	–
<i>S. notata</i>	1.2	$\pm$ 1.2	–	–	–	–	–	–	0.4	$\pm$ 0.4	–	–	–	–
<i>S. scrofa</i>	–	–	9.2	$\pm$ 9.2	–	–	–	–	–	–	–	–	–	–
<i>B. carolinensis</i>	–	–	27.7	$\pm$ 19.6	–	–	–	–	–	–	–	–	–	–
<i>A. hepsetus</i>	–	–	–	–	50.6	$\pm$ 35.1	–	–	–	–	–	–	–	–

brown meagres (*S. umbra*) have lost significance of the factor Region, while brown wrasse (*Labrus merula*) now present a significant regional effect, in that it was more abundant in region 3. Finally, two species (*S. cabrilla* and *C. julis*) lose the significance of the interaction Region  $\times$  Protection.

## Discussion

The present study shows that the western Mediterranean reef fish assemblage is patchy at a variety of spatial scales, from 10s of metres to 100s of kilometres. This

**Table 6** Mean value per 250-m<sup>2</sup> ( $\pm$  standard error of the mean, *SEM*), coefficient of variation (*CV*) and range of the variables describing habitat structure, and summary of the results from the spatial variation study (mixed analysis of variance), indicating the

factors at which significant variation exists. Sources of variation are as in Table 4. The abbreviations of habitat descriptors used in Tables 7 and 8, and Fig. 5 are also shown (*n* number, *m* metres, *ns* not significant; \**P* < 0.05, \*\**P* < 0.01, \*\*\**P* < 0.001)

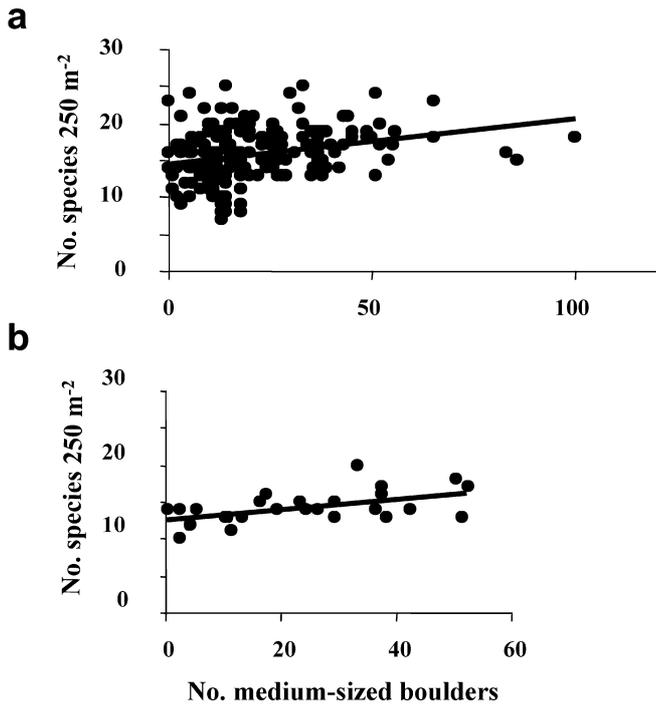
Habitat variables	Abbrev.	Mean	$\pm$ SEM	Range	CV	Signification of analysis				
						R	P	R $\times$ P	S(R $\times$ P)	Z(S(R $\times$ P))
Small boulders (n)	SMALL	47.1	$\pm$ 2.9	0–259	83.5	ns	ns	ns	**	ns
Medium-sized boulders (n)	MED	22.2	$\pm$ 1.2	0–100	74.2	ns	ns	ns	*	*
Large boulders (n)	LARGE	5.5	$\pm$ 0.3	0–30	85.1	ns	ns	ns	**	*
% <i>Posidonia oceanica</i>	POSI	25.6	$\pm$ 1.9	0–100	100.5	ns	ns	ns	**	***
% Sand	SAND	1.7	$\pm$ 0.4	0–30	285.0	ns	ns	ns	***	ns
% Rock	ROCK	72.6	$\pm$ 1.9	0–100	36.8	ns	ns	ns	ns	**
Minimum depth (m)	DMIN	9.8	$\pm$ 0.2	3–17	25.1	ns	ns	ns	**	*
Maximum depth (m)	DMAX	13.3	$\pm$ 0.2	5–20.5	22.7	ns	ns	ns	*	ns
Mean depth (m)	DMEAN	11.6	$\pm$ 0.2	4–18.8	22.0	ns	ns	ns	**	*
Verticality (m)	VERT	3.6	$\pm$ 0.2	0–11	59.7	*	ns	ns	ns	**

**Table 7** Summary of the results of multiple linear regression analyses for mean values of fish assemblage variables (considering all localities together, and by localities), indicating the independent variables included in each model (see Table 6 for abbreviations of variables) and the sign of their relationship. Quadratic and cubic terms of independent variables are indicated with a 2 or a 3 following the abbreviation (*ns* not significant; \**P* < 0.05, \*\**P* < 0.01, \*\*\**P* < 0.001)

Variable	Locality	Adj. <i>R</i> <sup>2</sup>	<i>P</i>	Variables included in the model
Species richness	All	0.18	**	DMAX + MED
	Cabo de Gata	–	ns	–
	Aguilas	–	ns	–
	Cabo de Palos	0.31	*	MED
	Isla Grosa	0.48	***	–SAND
	Cabrera	0.33	*	MED
	W Mallorca	–	ns	–
	Columbretes	–	ns	–
Mean abundance	All	0.18	***	SMALL – LARGE + MED2 + LARGE3 + ROCK3 + VERT2
	Cabo de Gata	–	ns	–
	Aguilas	0.25	**	VERT
	Cabo de Palos	0.61	***	–ROCK2 + ROCK3
	Isla Grosa	0.28	**	–MED
	Cabrera	–	ns	–
	W Mallorca	0.28	**	–POSI2-DMIN3
	Columbretes	–	ns	–
Mean biomass	All	0.09	*	SMALL + MED + ROCK3
	Cabo de Gata	–	ns	–
	Aguilas	0.37	**	VERT
	Cabo de Palos	0.16	*	MED3
	Isla Grosa	–	ns	–
	Cabrera	0.16	*	VERT3
	W Mallorca	–	ns	–
	Columbretes	–	ns	–
Diversity index <i>H'</i>	All	0.03	*	MEDIUM
	Cabo de Gata	–	ns	–
	Aguilas	–	ns	–
	Cabo de Palos	0.22	**	MEDIUM3
	Isla Grosa	0.19	*	SMALL
	Cabrera	–	ns	–
	W Mallorca	0.14	*	SMALL
	Columbretes	–	ns	–

study constitutes the first attempt to quantify this variability at a range of spatial scales in the Mediterranean Sea. A previous study (García-Charton and Pérez-Ruzafa 2001) quantified the spatial pattern of a fish assemblage at one of the localities considered here (Cabo de Palos), by detecting relevant scales of change at a continuous range of spatial scales from metres to 100s of metres, using autocorrelation analyses and Mantel tests. That method is complementary to the simultaneous multi-scale approach adopted here (Underwood and

Chapman 1996; García-Charton and Pérez-Ruzafa 1999). Although the unavoidable imposition of arbitrary scales (spatial factors) in the nested design implies problems linked to the possibility of introducing human biases, the “hierarchical” procedure allows us to sample a much larger spatial extent than the “continuous” one (10<sup>6</sup> m versus 10<sup>3</sup> m in our two studies), because in the former approach the data do not have to be collected continuously over the entire range of the study, as is the case for the latter method of spatial pattern analysis



**Fig. 4** Relationship between the number of fish species and the number of medium-sized boulders per 250-m<sup>2</sup> transect, showing the fitted linear-regression curve for **a** all localities together and **b** data from Cabo de Palos

(Underwood and Chapman 1996; García-Charton and Pérez-Ruzafa 2001). The multi-scale approach to studying fish assemblage patterns is the most precise way to obtain a realistic interpretation of spatial patterns when larger scales are to be considered.

#### The effect of fishing

Increase in abundance and/or biomass of target species, and of total abundance and biomass, is to be expected within MPAs due to the protection of critical spawning stock biomass from fishery depletion (Bohnsack 1996; Russ 2002). In our study, mean total abundance and biomass showed higher average values within MPAs. In the same way, abundance and biomass of several commercial fishes were consistently higher within protected areas compared to neighbouring unprotected sites, regardless of the geographical region. In addition, other commercial fishes were observed only inside MPAs, while still others showed a trend to higher abundance and biomass within MPAs. Our multi-reserve survey reaffirms the observations of other Mediterranean studies, performed in single marine reserves mostly in the north-western Mediterranean. For instance, Bell (1983) found that total density was significantly higher at the Cerbère–Banyuls marine reserve, and that species vulnerable to fishing were significantly more abundant within this protected site. Analogously, García-Rubies and Zabala (1990) observed that target species (except

*Serranus cabrilla* and *Mullus surmuletus*) were significantly more abundant inside than outside the Medes Islands natural park. Similar results were obtained by Francour (1994) in the Scandola marine reserve (Corsica), Harmelin et al. (1995) in Carry-le-Rouet marine reserve, and Macpherson et al. (2002) at the Medes Islands. In the same way, non-Mediterranean studies comparing protected sites with their unprotected counterparts find such an effect of protection on abundance and biomass of targeted fish species (see reviews by Russ 2002 and Halpern 2003, and references therein). Another expected effect of protection from fisheries is increasing species richness (e.g. Francour 1994; Jennings et al. 1996; McClanahan and Kaunda-Arara 1996; Wantiez et al. 1997; Russ and Alcalá 1998; Chiappone et al. 2000) as we have observed here.

Nevertheless, expected effects of protection are not always evident, since in our study some of the NRAs (e.g. Águilas) tended to have similar values of richness and abundance than MPAs, whereas in other MPAs (e.g. Cabrera) we censused abundances of some commercial species at least of the same magnitude as NRAs subject to high fishing pressure. Other studies observed an unclear response, as is the case of Dufour et al. (1995), who observed that, after 10 years of protection in Cerbère–Banyuls (i.e. compared to results of Bell 1983), total abundance decreased in the reserve, whereas it was maintained outside the reserve! In the same way, Roberts and Polunin (1992) in Ras Mohammed Marine Park (Egypt, Red Sea) found that several common, target species did not differ in abundance among fishing levels, and even that some of these species tended to present higher biomass in unfished sites. More recently, Valles et al. (2001) did not find significant differences in fish biomass inside and outside Virgin Islands National Park (Caribbean). Regarding the number of species, Roberts (1995) found that species richness per count did not differ between fished and unfished zones in Saba marine reserve (Netherlands Antilles). For their part, Rogers and Beets (2001) found observed differences in fish species richness not to be significant between inside and outside the Virgin Islands National Park (Caribbean). In the same way, Watson et al. (1996) observed that neither species number nor diversity of any family was affected by fishing pressure at several sites on the Kenyan coast (Indian Ocean). Also, Jennings and Polunin (1997) considered that observed differences in diversity by families among traditional protected areas in Kadavu Island (Fiji, tropical Pacific) were not attributable to differences in fishing intensity.

Observed regional variations among protected areas could be caused by differences in the time (1–9 years at the time of sampling) since the establishment of studied MPAs (Badalamenti et al. 2000; Francour et al. 2001). Some equivocal effects of protection on particularly targeted species (such as groupers) are probably due to these differences. Notably, recent data (García-Charton and Pérez-Ruzafa, in preparation) show a huge increase in abundance and biomass of dusky groupers

**Table 8** Value of adjusted  $R^2$  and significance (between brackets) of multiple linear regression analyses for mean values of abundance of the 26 most frequent, non-pelagic species, and of the spatial categories of Harmelin (1987) considering all localities together (indicating also the environmental

variables included in each model—see Table 6 for abbreviations of variables), and by localities. Quadratic and cubic terms of independent variables are indicated with a 2 or a 3 following the abbreviation (*ns* not significant; \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ )

	All localities		C. Gata	Aguilas	C. Palos	I. Grosa	Cabrera	W Mallorca	Columbretes
<i>M. helena</i>	MED+SMALL3+DMEAN3	0.19(**)	–	–	0.63(***)	–	–	–	–
<i>E. costae</i>	–MED+DMAX+SMALL2–ROCK2	0.19(***)	ns	–	–	–	–	–	–
<i>E. marginatus</i>	DMAX+SMALL3	0.08(***)	0.15(*)	–	–	–	ns	–	0.36(**)
<i>S. cabrilla</i>	–MED+DMIN	0.16(**)	0.11(*)	0.14(*)	0.37(**)	0.21(**)	ns	0.30(**)	0.37(**)
<i>S. scriba</i>	–	ns	ns	ns	0.12(*)	0.13(*)	ns	0.20(*)	ns
<i>A. imberbis</i>	–SAND+MED3–ROCK3+VERT2	0.20(***)	0.23(**)	0.49(***)	0.35(**)	0.70(***)	0.12(*)	0.18(*)	–
<i>S. umbra</i>	ROCK3+DMAX3	0.09(***)	–	–	–	–	–	–	0.15(*)
<i>M. surmuletus</i>	–	ns	0.66(***)	0.38(**)	–	0.37(***)	0.14(*)	–	–
<i>D. dentex</i>	MED+DMIN–ROCK2+ROCK3	0.22(***)	–	–	–	–	–	–	ns
<i>D. annularis</i>	–SMALL+MED–SAND–ROCK3	0.30(***)	–	0.41(***)	0.58(***)	0.47(***)	0.31(**)	0.40(***)	–
<i>D. puntazzo</i>	–LARGE+ROCK+VERT	0.13(***)	–	–	0.64(***)	0.37(***)	0.13(*)	–	–
<i>D. sargus</i>	MED2	0.03(**)	–	0.19(*)	ns	0.67(***)	ns	0.12(*)	–
<i>D. vulgaris</i>	ROCK+VERT3	0.08(***)	ns	ns	0.44(***)	0.55(***)	ns	0.10(*)	0.32(**)
<i>S. salpa</i>	MED–LARGE	0.07(***)	–	ns	ns	0.56(***)	ns	ns	0.39(***)
<i>S. cantharus</i>	DMIN+ROCK3	0.20(***)	–	–	–	–	0.25(**)	ns	ns
<i>C. chromis</i>	SMALL3+DMAX3	0.05(**)	ns	0.16(*)	0.48(***)	ns	ns	ns	ns
<i>C. julis</i>	SMALL–MED+SAND+MED3	0.13(***)	ns	0.31(**)	0.38(***)	ns	ns	0.32(**)	ns
<i>L. merula</i>	DMAX	0.03(**)	–	–	–	–	0.47(***)	–	ns
<i>S. doderleini</i>	POS12	0.14(***)	–	–	–	–	–	–	–
<i>S. mediterraneus</i>	LARGE+DMED	0.17***	0.21(*)	0.31(**)	–	–	0.12(*)	0.11(*)	ns
<i>S. melanorcercus</i>	–	ns	–	–	–	–	ns	ns	–
<i>S. ocellatus</i>	–	ns	ns	ns	ns	0.16(*)	ns	ns	ns
<i>S. roissali</i>	–DMED	0.06(***)	0.29(**)	0.72(***)	–	0.16(*)	0.13(*)	–	0.18(*)
<i>S. rostratus</i>	DMAX–ROCK3	0.12(***)	ns	ns	–	–	–	0.22(*)	–
<i>S. tinca</i>	LARGE–ROCK3	0.07(***)	ns	ns	0.36(***)	0.16(*)	ns	ns	ns
<i>T. pavo</i>	–LARGE	0.04(**)	0.50(***)	ns	0.41(***)	0.53(***)	0.43(**)	0.22(*)	ns
Category 1	MED	0.03(**)	0.15(*)	0.22(**)	0.28(**)	0.53(***)	0.43(***)	ns	0.29(**)
Category 2	–LARGE+SMALL2+ROCK3+VERT3	0.22(***)	ns	0.23(**)	0.71(***)	ns	0.18(*)	0.18(*)	ns
Category 3	MED–SAND	0.13(***)	0.15(*)	ns	0.39(**)	0.80(***)	ns	0.19(*)	ns
Category 4	–	ns	0.66(***)	0.38(**)	0.70(***)	0.37(***)	0.14(*)	0.28(**)	ns
Category 5	SMALL+SAND+DMAX2–DMAX3	0.14(***)	0.13(*)	ns	0.25(**)	0.21(*)	ns	0.14(*)	ns
Category 6	POS1+DMI+MED3+VERT2	0.21(***)	0.15(*)	0.33(**)	0.42(**)	0.63(***)	0.28(**)	0.66(***)	ns

(*Epinephelus marginatus*) in Cabo de Palos marine reserve after 7 years of protection, although there is a disparity in the response among sectors (Fig. 6). Therefore, in the present study, protection measures were too recent to produce positive effects in Cabo de Palos marine reserve. Consequently, it is apparent that the effects of protection of heavily harvested fish species in the Mediterranean become evident only after MPAs have been established for at least 3–4 years.

In addition, protected and non-protected areas differ in the accessibility of, and the exploitation intensity on, their fishing grounds (as a function of their distance from fishing harbours, density of the fishing fleets, etc.), as well as in the effectiveness of enforcement measures. Concerning the latter, most of the Mediterranean marine reserves are subject to insufficient enforcement measures, and some of them even have to be considered merely as "paper" reserves (Badalamenti et al. 2000). A recent study, using meta-analytical techniques, compared data for 19 marine reserves throughout the world (Côté et al. 2001), and concluded that the effect on fish abundance is highly variable, in relation to factors such

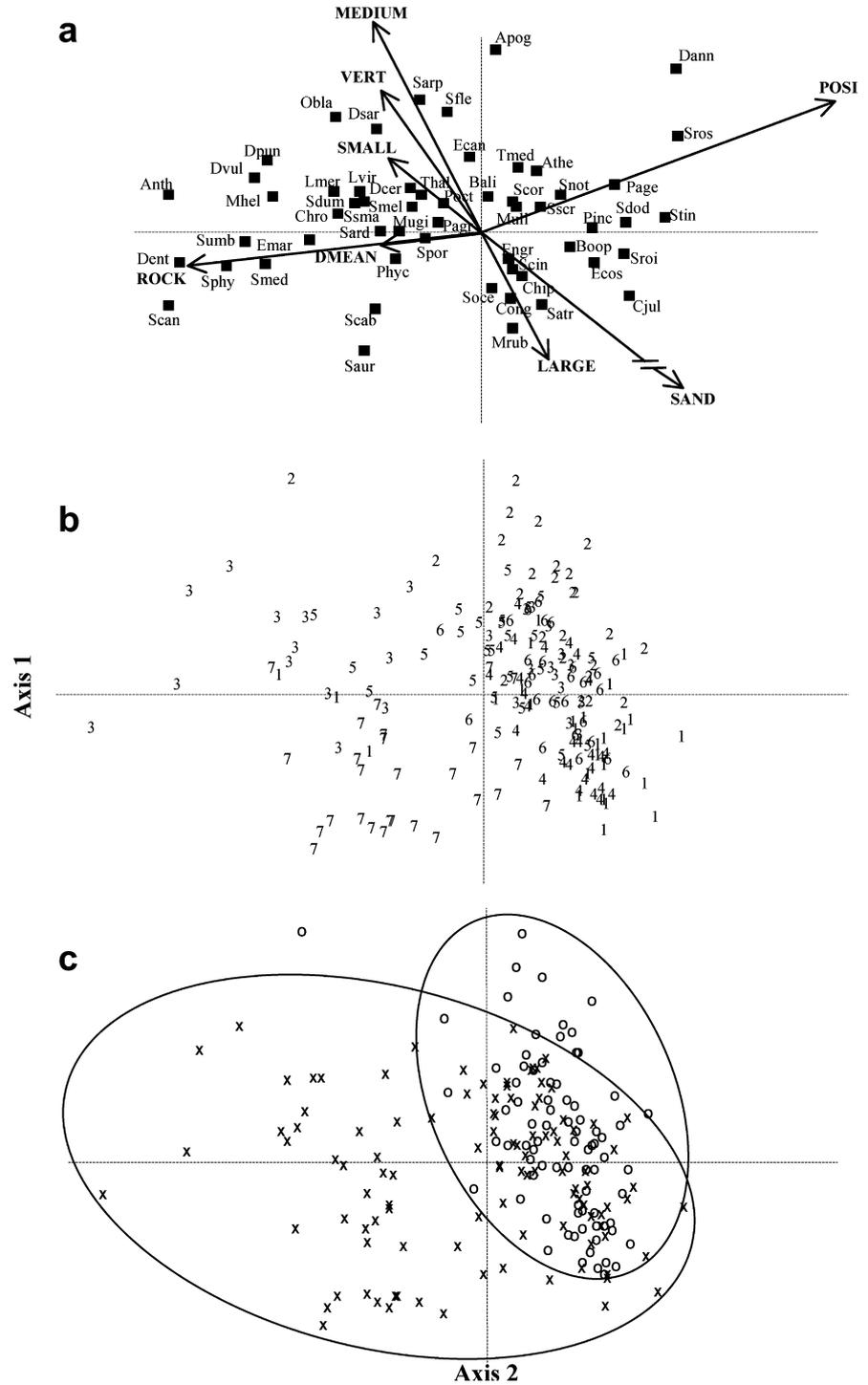
as intensity of exploitation outside protected areas, variation in enforcement efficiency, and habitat characteristics.

Comparisons among protected and fished areas have to be based on statistical tests that distinguish between "normal" variability and the influence of management (Allison et al. 1998). This variability can be due to several, non-exclusive causes (García-Charton and Pérez-Ruzafa 1999), such as large-scale climatic differences, variations in availability of habitat, food etc., and spatial variability of larval dynamics and recruitment, as discussed in the following sections.

#### Regional variation in fish assemblage

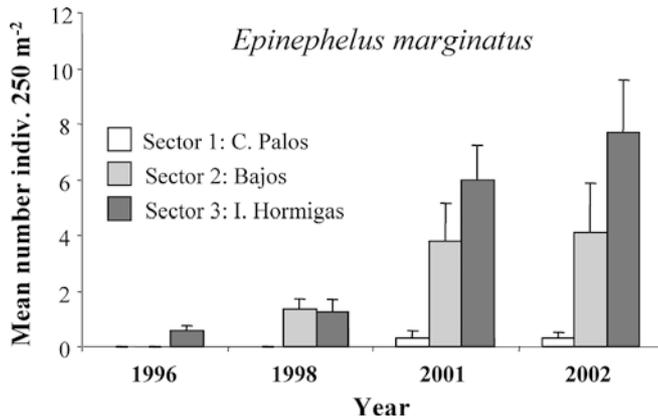
Under the assumption that fishes maximise the use of their food resources, observed geographical differences could be attributed in part to differential food availability in each locality, which in turn would depend on the local primary production and trophic structure, to determine the upper limit to the biomass that can be

**Fig. 5** Redundancy analysis biplot ordination diagram for habitat descriptors and fish species (**a**), and sampling units (**b** and **c**) using logged abundance data (see Tables 2 and 6 for abbreviations of species names and habitat descriptors, respectively). Localities are represented in **b** by numbers (1 Cabo de Gata, 2 Aguilas, 3 Cabo de Palos, 4 Isla Grosa, 5 Cabrera, 6 Mallorca, 7 Columbretes), and in **c** distinguishing between transects performed on protected (x) and unprotected (o) sites (both groups of sampling units are encircled)



maintained in a given area, i.e. the local carrying capacity (Christensen and Pauly 1992). Direct estimation of carrying capacity is extremely hard to make, however, because of the difficulties in quantifying the availability and quality of the huge variety of food and habitat required by all the species in a reef system (Edgar 1993). Instead, data on spatial variation in pelagic primary production could serve as an indication of food availability, since phytoplankton development is usually

correlated with abundance and distribution of zooplankton (Champalbert 1996) and successive trophic levels (Estrada 1996). A coincidence between spatial distribution of primary production and fish abundance and biomass seems to appear in our data. In effect, excluding pelagic and cryptic species, north-to-south and island-to-continent (as shown by the differences between the Balearic Islands and Columbretes) regional gradients of reef fish mean total abundance and biomass



**Fig. 6** Temporal evolution of the mean number of individuals per 250-m<sup>2</sup> ( $\pm$  SEM, n=9) of dusky groupers (*Epinephelus marginatus*) within the three sectors of the Cabo de Palos–Islas Hormigas marine reserve (SW Mediterranean) once the protection measures were established (in 1995) (see geographical location of the reserve and situation of the sectors in Fig. 1)

seem to occur, observed average values ranging from 93 to 247 individuals and from 5.8 to 31.2 kg 250-m<sup>-2</sup> among localities. The coincidence between fish data and measured primary production (see Material and methods section) is consistent with this “primary production hypothesis”. The direct relationship between pelagic primary production and fish biomass is corroborated by data of Caddy et al. (1995), who showed how a temporal trend in fish landings by Mediterranean fisheries is tracking a long-term trend in nutrient enrichment due to human activity (Béthoux et al. 1998). Also, an interaction between protection and food availability may occur (Pinnegar et al. 2000), so that primary and secondary productivity may increase inside marine reserves (Babcock et al. 1999). Studies of the trophic structure of fish assemblages, as well as the response of fishes to local (as produced, for instance, by the recent proliferation of extensive aquaculture farms on the Mediterranean coast) or regional variations of food availability, are needed to determine the magnitude of the effect of this factor.

The occurrence of infrequent (or rare) species determines most of the observed differences in species composition amongst localities. The causes of rarity can be multiple (Gaston 1994). Some species may be observed at the limit of their niche space, as could be the case in the occasional observation of swallowtail sea-perch (*Anthias anthias*) at Águilas, Cabo de Palos and Cabrera: although censuses were performed in shallow waters, some transects crossed rocky zones with a very steep topography, so that individuals of this species, identified as one of the few being exclusively sciaphilic (Harmelin 1990), were recorded swimming at the upper limit of their depth distribution. Some other species could be rare because our study area includes the limit of their geographical range. Most of these species have warm-Atlantic affinities, and show a gradient of abundance from the eastern Atlantic Ocean to the northern

part of the western Mediterranean basin. For instance, blacktail comber (*Serranus atricauda*) presents a density of 0.7 individuals 250-m<sup>-2</sup> in the Canary Islands (Falcón et al. 1996), and even higher in Selvagens, Madeira and Açores Islands (Falcón and García-Charton, unpublished data). In the present study the abundance of this species goes from 0.3 individuals 250-m<sup>-2</sup> at Cabo de Gata to 0.04 individuals 250-m<sup>-2</sup> at Cabo de Palos, which is the northernmost locality in which we have recorded this species. As another example, African striped grunt (*Parapristipoma octolineatum*) is common in the archipelago of Cabo Verde (Falcón and García-Charton, unpublished data); is present in the Canary Islands (Falcón et al. 1996), African coast, Madeira and Portugal (Ben-Tuvia and McKay 1986); and in this study it was observed forming shoals of tens of individuals only at Cabo de Gata (3.5 individuals 250-m<sup>-2</sup>) and Águilas (0.3 individuals 250-m<sup>-2</sup>). Previous studies have detected solitary individuals of *P. octolineatum* at Cabo Palos (García-Charton and Pérez-Ruzafa 1998) and at Santa Pola (Alicante, SE Spain) (Bayle-Sempere 1999; García-Charton, personal observation). Other “thermophilic” species showing this latitudinal gradient of abundance in this study were bastard grunt (*Pomadasyss incisus*), golden grouper (*Epinephelus costae*), dogtooth grouper (*Epinephelus caninus*), zebra sea-bream (*Diplodus cervinus*), and Doderlein’s wrasse (*Symphodus doderleini*). Other species were present at all localities, but were much more abundant in southern ones, as the ornate wrasse (*Thalassoma pavo*), ranging from 6.6 to 99.1 individuals 250-m<sup>-2</sup> in the latitudinal gradient studied here, as observed also by Guidetti et al. (2002). Other species showed the opposite trend, such as black sea-bream (*Spondyliosoma cantharus*), which is far more abundant in northern localities. Hydroclimatic characteristics in relation to individual and species-specific thermal tolerances (Moyle and Cech 2000) have been found to be a key factor for understanding faunistic affinities between marine coastal areas (Longhurst 1998). Water temperature can influence fish distribution through its effect on the molecular biology and metabolism (Love 1974; Goldspink 1995; Shulman and Love 1999), on mortality, and on growth and reproductive rates of individuals (Houde 1989; Planes et al. 1999; Pörtner et al. 2001). Therefore, variations in seawater temperature in the western Mediterranean basin are likely to be partially responsible for the observed geographical differences.

#### The relative importance of habitat structure

Habitat structure is one of the factors likely to explain the variability of Mediterranean fish assemblages, at least for some species and assemblage parameters (García-Charton et al. 2000). Other studies attribute to habitat a substantial part of the observed variation in abundance, richness and species composition (García-Charton and Pérez Ruzafa 1998, 2001). Previous studies

in the Mediterranean assumed the importance of habitat, but did not provide data to support it (e.g. Bell 1983; Harmelin 1987, 1990; García-Rubies and Zabala 1990; Dufour et al. 1995; Spyker and van den Berghe 1995; Reñones et al. 1997). The importance of habitat structure in determining small-scale spatial variability in fish assemblages has been shown both in temperate (e.g. Connell and Jones 1991; Norton 1991; Holbrook et al. 1992; Lowry and Suthers 1999) and tropical areas (e.g. Luckhurst and Luckhurst 1978; Grigg 1994; McGehee 1994; Jennings et al. 1996; Chabanet et al. 1995; Ault and Johnson 1998; Friedlander and Parrish 1998).

There is a source of confounding in the fact that, usually, Mediterranean marine reserves are established in zones that already harbour structurally complex habitats, which form favourable habitats for the development of a rich and abundant reef fish fauna (García-Charton and Pérez-Ruzafa 1999). In our data, part of the observed variability in fish assemblage structure could be due to this selection of areas to be protected that are particularly favourable to high fish abundance and diversity, because they offer predominantly rocky, complex habitats. Nevertheless, the influence of habitat structure seems to be exerted mainly at small-to-intermediate spatial scales, since, in the present study, extraction of variation due to habitat from the variables chosen as indicators of the “reserve effect” produces mainly the loss of heterogeneity among sectors and/or zones. Differences in abundance at these small scales can be due in part to local habitat requirements for those species that need a heterogeneous habitat, with an important proportion of *Posidonia* and/or sand in the rocky matrix, to settle or live as juveniles or adults, as shown by redundancy analysis. The most obvious example of this pattern is the annular sea bream (*Diplodus annularis*), which has not been observed in Columbretes, where the seagrass *Posidonia oceanica* is absent. Other species frequently found in heterogeneous habitats are sea breams (*Diplodus* spp., *Sarpa salpa*, *Pagrus pagrus*), wrasses (*Symphodus* spp., *Labrus* spp., *Coris julis*) and red mullets (*Mullus surmuletus*) (Francour and Le Diréac’h 1994; García-Rubies and Macpherson 1995; Harmelin-Vivien et al. 1995; Vigliola et al. 1998; García-Charton and Pérez-Ruzafa 2001; Vigliola and Harmelin-Vivien 2001). Studies describing fish assemblages at multiple scales (e.g. Williams and Hatcher 1983; Galzin 1987; Holbrook et al. 2000; Gust et al. 2001) usually favour the influence of habitat to explain small-to-medium patchiness (Williams 1991). Distinguishing the relative contribution of habitat structure can help to elucidate the actual effects of protection (Jennings et al. 1996).

Nevertheless, in some cases, it is difficult with our data to decide what environmental variables are important for particular species or spatial categories, in view of the fact that there is no consistency in the regression models among localities for most parameters. One “null” explanation for this pattern is that fish species have homologous habitat requirements, but the

number of sampling units—27 50×5-m<sup>2</sup> transects (covering 6,750 m<sup>2</sup>) per locality—would not be sufficient to capture the “environmental spectrum” at each locality, despite the huge sampling effort developed, leading to biased fish–habitat relationships within each locality. The alternative would be that, effectively, fish species have different habitat associations depending on the locality. Flexibility in habitat use by fish species could then be important, by enabling fishes to adapt to the resources available at each locality, and by this means to avoid competition for resources, as argued by García-Charton and Pérez-Ruzafa (2001). Co-ordinated, large-scale monitoring would be necessary to distinguish between both possibilities.

#### Spatial variations in larval dynamics and recruitment

Large-scale spatial variability in larval distribution, occurrence of settlement episodes and/or post-settlement survival could also be partially responsible for the geographical differences in species abundance among the studied localities. The horizontal distribution of fish larvae has been reported to be highly variable in the Mediterranean (Sabatés 1990; Olivar and Sabatés 1997). This variability is generally related to mesoscale hydrographic variability (see review by Planes et al. 2000). In the Mediterranean, seasonal fronts (Masó and Tintoré 1991; Sabatés and Olivar 1996; Masó et al. 1998) and transitory hydrographic structures (Olivar et al. 1998) can explain in part the distribution of fish larvae, which can also be altered by differences in larval ecology among fish species (duration of pelagic larval stage, swimming capabilities, etc.) (Planes et al. 2000). Significant differences in density of settlers among localities separated by 10s to 100s of kilometres have been reported for sparids, and these large-scale spatial differences predominate over changes between years (Vigliola et al. 1998). Large-scale hydrodynamic features leading to differential abundance of larvae, or site-specific differences in mortality (Macpherson et al. 1997, 2000; Planes et al. 1998) and/or growth (Planes et al. 1999) of juveniles, can partially explain the observed differences among localities.

Differential settlement among sites separated by kilometres, as observed by Vigliola et al. (1998), could also affect fish assemblage variability at small-to-medium scales. These differences could be due to micro-habitat preferences of settlers (García-Rubies and Macpherson 1995; Harmelin-Vivien et al. 1985; Macpherson 1998), but several lines of evidence do not support the prevalence of habitat to explain recruitment variation at small-to-medium scales. Firstly, inter-annual variability in recruitment of sparids is very important at small spatial scales (Vigliola et al. 1998), so that it would be determined mainly by larval dynamics, which in turn depend on the reproductive success at the regional scale, larval mortality, and the general hydrodynamic regime. In addition, juvenile mortality seems to be

a density-dependent process (Macpherson et al. 1997; Planes et al. 1998), conferring predominance on post-recruitment processes such as predation and competition for the available resources (Jones 1991). In any case, much more effort is needed in the Mediterranean to determine the larval dynamics, settlement variability at different spatial and temporal scales, and the relative importance of post-settlement events in the variability of adult reef fish populations.

#### Abundance versus biomass data

Using biomass rather than abundance data gave slightly different results when characterising the differences at the three spatial scales considered. This is probably due to the great variety of body sizes among the species considered: for instance, some of the species showing differences in abundance, but not in biomass with respect to the protection level, were relatively large-sized (usually >20 cm) and of solitary or small-number-shoaling habits (e.g. *Epinephelus* spp., *Sciaena umbra*), so that their rank is more important when measured by biomass. Nevertheless, the multivariate analyses (RDA) were very similar whether using abundance or biomass data, conferring robustness on their interpretation, especially if we consider that the environmental gradient is short, and that the data are likely to be “noisy”. In effect, Bianchi and Høisaeter (1992) concluded that, where ecological gradients are short and the individual fish sizes are different, there might be a marked difference in the patterns shown by abundance and biomass data, which is not the case in our results. We argue that it is important to consider both abundance and biomass values when exploring spatial differences of fish assemblages.

#### Conclusion

Causes of the observed patchiness of Mediterranean reef fish assemblages are probably multiple, from the time when the larvae arrive from the plankton, to processes operating after the settlement. Overall, our study suggests that, superimposed on differences due to protection, habitat structure and hydrographical differences are likely to be the significant factors in the observed variability, but most of the information needed to estimate the relative importance of these environmental variables against other factors—that is, larval dynamics, recruitment variability, and interspecific interactions (and physical factors that determine them, as water currents)—is scarce and usually relative to only a few species (as sparids). Therefore, long-term, multi-scale spatial and temporal monitoring of Mediterranean reef fish assemblages, as well as small-to-medium scale process-oriented manipulative experiments are urgently needed to fully understand patterns among reef fish assemblages.

Most studies that aim at determining the effects of marine reserves are based on the comparison of one protected area with one or several adjacent non-protected areas. This study shows that spatial variability of variables used as indicators of success of protection measures is very high, thus making it difficult to properly assess protection effects. Moreover, when evaluating the effect of fishing and other human factors, temporal variability (from small-scale fluctuations to long-term variations) has also to be considered in order to avoid confounding (García-Charton and Pérez-Ruzafa 1999). Only in some cases has adequate spatial and/or temporal replication been accomplished (Russ 2002). If “reserve effects” are to be correctly identified and reliably predicted, sampling and monitoring designs involving considerable replication in space and time are essential (García-Charton et al. 2000). The increase in the number of samples and/or the spatial replication with nested factors facilitates the interpretation of the observed spatial heterogeneity of fish population at different spatial scales. One way to facilitate the study of the effect of marine reserves in the future is to use data sets such as those presented here to optimise sampling designs through simulation and power analysis, in order to improve the capability of any given sampling design to detect impacts of a specified magnitude (Benedetti-Cecchi 2001).

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#### References

- Allen TFH, Hoekstra TW (1991) Role of heterogeneity in scaling of ecological systems under analysis. In: Kolasa J, Pickett STA (eds) Ecological heterogeneity. Springer, New York Berlin Heidelberg, pp 47–68
- Allison GW, Lubchenco J, Carr MH (1998) Marine reserves are necessary but not sufficient for marine conservation. *Ecol Appl* 8:79–92
- Alvarez A, Tintoré J, Sabatés A (1996) Flow modification and shelf-slope exchange induced by a submarine canyon off the northeast Spanish coast. *J Geophys Res* 101:12043–12055
- Analytical Software (1992) STATISTIX 4.0: an interactive analysis program for the IBM PC
- Ault TR, Johnson CR (1998) Spatially and temporally predictable fish communities on coral reefs. *Ecol Monogr* 68:25–50
- Babcock R, Kelly S, Shears NT, Walker JW, Willis TJ (1999) Changes in community structure in temperate marine reserves. *Mar Ecol Prog Ser* 189:125–134

- Badalamenti F, Ramos AA, Voultziadou E, Sánchez-Lisaso JL, D'Anna G, Pipitone C, Mas J, Ruiz-Fernández JM, Whitmarsh D, Riggio S (2000) Cultural and socio-economic impacts of Mediterranean marine protected areas. *Environ Conserv* 27:110–125
- Bayle-Sempere JT (1999) Ictiofauna de la Reserva Marina de Tabarca (Alicante, Sudeste Ibérico): evaluación de las medidas de protección. PhD Thesis, University of Alicante (Spain)
- Bayle-Sempere JT, Valle C, Verdú A (2002) ecoCEN: application for managing data from fish visual counts. FAO COPEMED Series no. 7
- Bell JD (1983) Effects of depth and marine reserve fishing restrictions on the structure of a rocky reef fish assemblage in the north-western Mediterranean Sea. *J Appl Ecol* 20:357–369
- Bell JD, Craik GJS, Pollard DA, Russell BC (1985) Estimating length frequency distributions of large reef fish under water. *Coral Reefs* 4:41–44
- Ben-Tuvia A, McKay R (1986) Haemulidae. In: Whitehead PJP, Bauchot ML, Hureau JC, Nielsen J, Tortonese E (eds) *Fishes of the North-eastern Atlantic and the Mediterranean*. UNESCO, Paris, pp 858–864
- Benedetti-Cecchi L (2001) Beyond BACI: optimization of environmental sampling designs through monitoring and simulation. *Ecol Appl* 11:783–799
- Béthoux JP, Morin P, Chaumery C, Connan O, Gentili B, Ruiz-Pino D (1998) Nutrients in the Mediterranean Sea, mass balance and statistical analysis of concentrations with respect to environmental change. *Mar Chem* 63:155–169
- Bianchi G, Hoisaeter T (1992) Relative merits of using numbers and biomass in fish community studies. *Mar Ecol Prog Ser* 85:25–33
- Bohnsack JA (1996) Maintenance and recovery of reef fishery productivity. In: Polunin NVC, Roberts CM (eds) *Reef fisheries*. Chapman and Hall, London, pp 283–313
- Booth DJ, Brosnan DM (1995) The role of recruitment dynamics in rocky shore and coral reef fish communities. *Adv Ecol Res* 26:309–385
- Braak CJF ter (1990) Update notes: CANOCO v. 3.10. Agricultural Mathematics Group, Wageningen, The Netherlands
- Braak CJF ter, Prentice IC (1988) A theory of gradient analysis. *Adv Ecol Res* 18:271–317
- Caddy JF, Refk R, Do-Chi T (1995) Productivity estimates for the Mediterranean: evidence of accelerating ecological change. *Ocean Coast Manage* 26:1–18
- Cadoret L, Adjeroud M, Tsuchiya M (1999) Spatial distribution of chaetodontid fish in coral reefs of the Ryuku Islands, southern Japan. *J Mar Biol Assoc UK* 79:725–735
- Chabanet P, Dufour V, Galzin R (1995) Disturbance impact on reef fish communities in Reunion Island (Indian Ocean) *J Exp Mar Biol Ecol* 188:29–48
- Champalbert G (1996) Characteristics of zooplankton standing stock and communities in the western Mediterranean Sea: relations to hydrology. *Sci Mar* 60 [Suppl. 2]:97–113
- Chapman MR, Kramer DL (1999) Gradients in coral reef fish density and size across the Barbados Marine Reserve boundary: effects of reserve protection and habitat characteristics. *Mar Ecol Prog Ser* 181:81–96
- Chiappone M, Sluka R, Sealey KS (2000) Groupers (Pisces: Serranidae) in fished and protected areas of the Florida Keys, Bahamas and northern Caribbean. *Mar Ecol Prog Ser* 198:261–272
- Christensen V, Pauly D (1992) ECOPATH II—a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecol Model* 61:169–185
- Connell SD, Jones GP (1991) The influence of habitat complexity on postrecruitment processes in a temperate reef fish population. *J Exp Mar Biol Ecol* 51:271–294
- Côté IM, Mosqueira I, Reynolds JD (2001) Effects of marine reserve characteristics on the protection of fish populations: a meta-analysis. *J Fish Biol* 59 [Suppl A]:178–189
- Crise A, Allen JJ, Baretta J, Crispi G, Masetti R, Solidoro C (1999) The Mediterranean pelagic ecosystem response to physical forcing. *Prog Oceanogr* 44:219–243
- Dayton PK, Tegner MJ (1984) The importance of scale in community ecology: a kelp forest example with terrestrial analogs. In: Price PW, Slobodkinoff CN, Gaud WS (eds) *A new ecology: novel approaches to interactive systems*. Wiley, New York, pp 457–481
- Dufour V, Jouvenel J-Y, Galzin R (1995) Study of a Mediterranean reef fish assemblage: comparisons of population distributions between depths in protected and unprotected areas over one decade. *Aquat Living Resour* 8:17–25
- Edgar GJ (1993) Measurement of the carrying capacity of benthic habitats using a metabolic-rate based index. *Oecologia* 95:115–121
- Estrada M (1981) Biomasa fitoplanctónica y producción primaria en el Mediterráneo occidental a principios de otoño. *Invest Pesq* 45:211–230
- Estrada M (1996) Primary production in the northwestern Mediterranean. *Sci Mar* 60 [Suppl. 2]:5–64
- Estrada M, Vives F, Alcaraz M (1985) Life and the productivity of the open sea. In: Margalef R (ed) *Western Mediterranean*. Pergamon Press, Oxford, p 148–197
- Falcón JM, Bortone SA, Brito A, Bundrick CM (1996) Structure of and relationships within and between the littoral, rock-substrate fish communities off four islands in the Canarian Archipelago. *Mar Biol* 125:215–231
- Font J, Salat J, Tintoré J (1988) Permanent features of the circulation in the Catalan Sea. *Oceanol Acta Spec* 9:51–57
- Fowler AJ, Doherty PJ, Williams DM (1992) Multi-scale analysis of recruitment of a coral reef fish on the Great Barrier Reef. *Mar Ecol Prog Ser* 82:131–141
- Francour P (1994) Pluriannual analysis of the reserve effect on ichthyofauna in the Scandola natural reserve (Corsica, Northwestern Mediterranean). *Oceanol Acta* 17:309–317
- Francour P, Le Diréac'h L (1994) Recrutement de l'ichtyofaune dans l'herbier superficiel à *Posidonia oceanica* de la Réserve Naturelle de Scandola (Corse, Méditerranée nord-occidentale): Données préliminaires. *Trav Sci Parc Natl Reg Res Nat Corse Fr* 46:71–91
- Francour P, Harmelin J-G, Pollard D, Sartoretto S (2001) A review of marine protected areas in the northwestern Mediterranean region: siting, usage, zonation and management. *Aquat Conserv Mar Freshw Ecosyst* 11:155–188
- Friedlander AM, Parrish JD (1998) Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *J Exp Mar Biol Ecol* 224:1–30
- Galzin R (1987) Structure of fish communities of French Polynesian coral reefs. I. Spatial scales. *Mar Ecol Prog Ser* 41:129–136
- Galzin R, Planes S, Dufour V, Salvat B (1994) Variation in diversity of coral reef fish between French Polynesian atolls. *Coral Reefs* 13:175–180
- García-Charton JA, Pérez-Ruzafa A (1998) Correlation between habitat structure and a rocky reef fish assemblage in SW Mediterranean. *PSZN I, Mar Ecol* 19:111–128
- García-Charton JA, Pérez-Ruzafa A (1999) Ecological heterogeneity and the evaluation of the effects of marine reserves. *Fish Res* 42:1–20
- García-Charton JA, Pérez-Ruzafa A (2001) Spatial pattern and the habitat structure of a Mediterranean rocky reef fish local assemblage. *Mar Biol* 138:917–934
- García-Charton JA, Williams I, Pérez-Ruzafa A, Milazzo M, Chemello R, Marcos C, Kitsos M-S, Koukouras A, Riggio S (2000) Evaluating the ecological effects of Mediterranean marine reserves: habitat, scale and the natural variability of ecosystems. *Environ Conserv* 27:159–178
- García-Rubies A, Macpherson E (1995) Substrate use and temporal pattern of recruitment in juvenile fishes of the Mediterranean littoral. *Mar Biol* 124:35–42
- García-Rubies A, Zabala M (1990) Effects of total fishing prohibition on the rocky fish assemblages of Medes Islands marine reserve (NW Mediterranean). *Sci Mar* 54:317–328
- Gaston KJ (1994) *Rarity*. Chapman and Hall, London
- Gladfelter WB, Ogden JC, Gladfelter EH (1980) Similarity and diversity among coral reef fish communities: a comparison between tropical Western Atlantic (Virgin Islands) and tropical

- Central Pacific (Marshall Islands) patch reefs. *Ecology* 61:1156–1168
- Goldspink G (1995) Adaptation of fish to different environmental temperature by qualitative and quantitative changes in gene expression. *J Therm Biol* 20:167–174
- Grigg RW (1994) Effects of sewage discharge, fishing pressure and habitat complexity on coral ecosystems and reef fishes in Hawaii. *Mar Ecol Prog Ser* 103:25–34
- Guidetti P, Bianchi CN, La Mesa G, Modena M, Morri C, Sarà G, Vacchi M (2002) Abundance and size structure of *Thalassoma pavo* (Pisces: Labridae) in the western Mediterranean Sea: variability at different spatial scales. *J Mar Biol Assoc UK* 82:495–500
- Gust N, Choat JH, McCormick MI (2001) Spatial variability in reef fish distribution, abundance, size and biomass: a multi-scale analysis. *Mar Ecol Prog Ser* 214:237–251
- Halpern B (2003) The impact of marine reserves: do reserves work and does reserve size matter? *Ecol Appl* 13:117–137
- Harmelin J-G (1987) Structure et variabilité de l'ichtyofaune d'une zone rocheuse protégée en Méditerranée (Parc national de Port-Cros, France). *PSZN I, Mar Ecol* 8:263–284
- Harmelin J-G (1990) Ichtyofaune des fonds rocheux de Méditerranée: structure du peuplement du coralligène de l'île de Port-Cros (Parc national, France). *Mésogée* 50:23–30
- Harmelin J-G, Bacht F, Garcia F (1995) Mediterranean marine reserves: fish indices as tests of protection efficiency. *PSZN I, Mar Ecol* 16:233–250
- Harmelin-Vivien ML, Harmelin J-G, Chauvet C, Duval C, Galzin R, Lejeune P, Barnabé G, Blanc F, Chevalier R, Duclerc J, Lasserre G (1985) Evaluation des peuplements et populations de poissons. Méthodes et problèmes. *Rev Ecol (Terre Vie)* 40:467–539
- Harmelin-Vivien ML, Harmelin J-G, Leboulloux V (1995) Microhabitat requirements for settlement of juvenile sparid fishes on Mediterranean rocky shores. *Hydrobiologia* 300/301:309–320
- Hewitt JE, Thrush SF, Cummings VJ, Turner SJ (1998) The effect of changing sampling scales on our ability to detect effects of large-scale processes on communities. *J Exp Mar Biol Ecol* 227:251–264
- Hixon MA (1991) Predation as a process structuring coral reef fish communities. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, New York, p 475–508
- Holbrook SJ, Swarbrick SL, Schmitt RJ, Ambrose RF (1992) Reef architecture and reef fish: correlations of population densities with attributes of subtidal rocky environments. In: Battershill CN, Schiel DR, Jones GP, Creese RG, MacDiarmid AB (eds) *Proceedings of the Second International Temperate Reef Symposium, 7–10 January 1992, Auckland, New Zealand*. NIWA Marine, Wellington, NZ, pp 99–106
- Holbrook SJ, Schmitt RJ, Stephens JA Jr (1997) Changes in an assemblage of temperate reef fishes associated with a climate shift. *Ecol Appl* 7:1299–1310
- Holbrook SJ, Forrester GE, Schmitt RJ (2000) Spatial patterns in abundance of a damselfish reflect availability of suitable habitat. *Oecologia* 122:109–120
- Houde ED (1989) Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. *Fish Bull US* 87:471–495
- Jennings S, Polunin NVC (1997) Impacts of predator depletion by fishing on the biomass and diversity of non-target reef fish communities. *Coral Reefs* 16:71–82
- Jennings S, Boullé DP, Polunin NVC (1996) Habitat correlates of the distribution and biomass of Seychelles' reef fishes. *Environ Biol Fish* 46:15–25
- Jones GP (1991) Postrecruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, New York, pp 294–328
- Kotliar NB, Wiens JA (1990) Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59:253–260
- La Mesa G, Vacchi M (1999) An analysis of the coastal fish assemblage of the Ustica Island Marine Reserve (Mediterranean Sea). *PSZN I, Mar Ecol* 20:147–165
- Leis JM, McCormick MI (2002) The biology, behavior, and ecology of the pelagic, larval stage of coral reef fishes. In: Sale PF (ed) *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, New York, pp 171–199
- Lefèvre D, Minas HJ, Minas M, Robinson C, Williams P J Le B, Woodward EMS (1997) Review of gross community production, primary production, net community production and dark community respiration in the Gulf of Lions. *Deep-Sea Res Part II* 44:521–950
- Levin SA (1992) The problem of pattern and scale in ecology. *Ecology* 73:1943–1967
- Lincoln Smith MP (1989) Improving multispecies rocky reef fish censuses by counting different groups of species using different procedures. *Environ Biol Fish* 26:29–37
- Lincoln Smith MP, Bell JD, Hair CA (1991) Spatial variation in abundance of recently settled rocky reef fish in southeastern Australia: implications for detecting change. *Mar Ecol Prog Ser* 77:95–103
- Longhurst A (1998) *Ecological geography of the sea*. Academic Press, San Diego
- Love RM (1974) *The chemical biology of fishes*. Academic Press, London
- Lowry MB, Suthers IM (1999) Home range, activity and distribution patterns of a temperate rocky-reef fish, *Cheilodactylus fuscus*. *Mar Biol* 132:569–578
- Luckhurst BE, Luckhurst K (1978) Analysis of the influence of substrate variables on coral reef fish communities. *Mar Biol* 49:317–323
- Macpherson E (1998) Ontogenetic shifts in habitat use and aggregation in juvenile sparid fishes. *J Exp Mar Biol Ecol* 220:127–150
- Macpherson E, Biagi F, Francour P, García-Rubies A, Harmelin J, Harmelin-Vivien M, Jouvenel JY, Planes S, Vigliola L, Tunesi L (1997) Mortality of juvenile fishes of the genus *Diplodus* in protected and unprotected areas in the western Mediterranean Sea. *Mar Ecol Prog Ser* 160:135–147
- Macpherson E, García-Rubies A, Gordo A (2000) Direct estimation of natural mortality rates for littoral marine fishes using population data from a marine reserve. *Mar Biol* 137:1067–1076
- Macpherson E, Gordo A, García-Rubies A (2002) Biomass size spectra in littoral fishes in protected and unprotected areas in the NW Mediterranean. *Estuar Coast Shelf Sci* 55:777–788
- Masó M, Tintoré J (1991) Variability of the shelf water off the northeast Spanish coast. *J Mar Syst* 1:441–450
- Masó M, Sabatés A, Olivar MP (1998) Short-term physical and biological variability in the shelf-slope region of the NW Mediterranean during the spring transition period. *Cont Shelf Res* 18:661–675
- Masó M, Tintoré J, La Violette PE (1990) Coastal flow modification by submarine canyons along the northwestern Mediterranean. *Sci Mar* 54:343–348
- McClanahan TR, Kaunda-Arara B (1996) Fishery recovery in a coral-reef marine park and its effect on the adjacent fishery. *Conserv Biol* 10:1187–1199
- McCullagh P, Nelder JA (1989) *Generalized linear models*, 2nd edn. Chapman and Hall, New York
- McGehee MA (1994) Correspondence between assemblages of coral reef fishes and gradients of water motion, depth, and substrate size off Puerto Rico. *Mar Ecol Prog Ser* 105:243–255
- Millot C (1987) Circulation in the Mediterranean Sea. *Oceanol Acta* 10:143–149
- Mouillot D, Culioli J-M, Lepretre A, Tomasini J-A (1999) Dispersion statistics and sample size estimates for three fish species (*Symphodus ocellatus*, *Serranus scriba* and *Diplodus annularis*) in the Lavezzi Islands Marine Reserve (South Corsica, Mediterranean Sea). *PSZN I, Mar Ecol* 20:19–34
- Moyle PB, Cech JJ Jr (2000) *Fishes: an introduction to ichthyology*. Prentice-Hall, Upper Saddle River, N.Y.

- Norton SF (1991) Habitat use and community structure in an assemblage of cottid fishes. *Ecology* 72:2181–2192
- Olivar MP, Sabatés A (1997) Vertical distribution of fish larvae in the north-west Mediterranean Sea in spring. *Mar Biol* 129:289–300
- Olivar MP, Sabatés A, Abelló P, García M (1998) Transitory hydrographic structures and distribution of fish larvae and neustonic crustaceans in the north-western Mediterranean. *Oceanol Acta* 21:95–104
- Pinnegar JK, Polunin NVC, Francour P, Badalamenti F, Chemello R, Harmelin-Vivien M, Hereu B, Milazzo M, D'Anna G, Pipitone C (2000) Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. *Environ Conserv* 27:179–200
- Planes S, Lefèvre A, Legendre P, Galzin R (1993) Spatio-temporal variability in fish recruitment to a coral reef (Moorea, French Polynesia). *Coral Reefs* 12:105–113
- Planes S, Jouvenel JY, Lenfant P (1998) Density dependence in post-recruitment processes of juvenile sparids in the littoral of the Mediterranean Sea. *Oikos* 83:293–300
- Planes S, Macpherson E, Biagi F, García-Rubies A, Harmelin J, Harmelin-Vivien M, Jouvenel J-Y, Tunesi L, Vigliola L, Galzin R (1999) Spatio-Temporal variability in growth of juvenile sparid fishes in the Mediterranean infralittoral zone. *J Mar Biol Assoc UK* 79:137–143
- Planes S, Galzin R, García-Rubies A, Goñi R, Harmelin J-G, Le Diréac'h L, Lenfant P, Quetglas A (2000) Effects of marine protected areas on recruitment processes with special reference to Mediterranean littoral ecosystems. *Environ Conserv* 27:126–143
- Pörtner HO, Berdal B, Blust R, Brix O, Colosimo A, De Wachter B, Giuliani A, Johansen T, Fischer T, Knust R, Lannig G, Naevdal G, Nedenes A, Nyhammer G, Sartoris FJ, Serendero I, Sirabella P, Thorkildsen S, Zakhartsev M (2001) Climate-induced temperature effects on growth performance, fecundity and recruitment in marine fish: developing a hypothesis for cause and effect relationships in Atlantic cod (*Gadus morhua*) and common eelpout (*Zoarces viviparus*). *Cont Shelf Res* 21:1975–1997
- Reñones O, Moranta J, Coll J, Morales-Nin B (1997) Rocky bottom fish communities of Cabrera Archipelago National Park (Mallorca, western Mediterranean). *Sci Mar* 61:495–506
- Roberts CM (1995) Rapid build-up of fish biomass in a Caribbean marine reserve. *Conserv Biol* 9:815–826
- Roberts CM, Polunin NVC (1992) Effects of marine reserve protection on northern Red Sea fish populations. *Proc 7th Int Coral Reef Symp* 2:969–977
- Roberts CM, Shepherd ARD, Ormond RFG (1992) Large-scale variation in assemblage structure of Red Sea butterflyfishes and angelfishes. *J Biogeogr* 19:239–250
- Rogers CS, Beets J (2001) Degradation of marine ecosystems and decline of fishery resources in marine protected areas in the US Virgin Islands. *Environ Conserv* 28:312–322
- Russ G (1984a) Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. I. Levels of variability across the entire continental shelf. *Mar Ecol Prog Ser* 20:23–34
- Russ G (1984b) Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. II. Patterns of zonation of mid-shelf and outershelf reefs. *Mar Ecol Prog Ser* 20:35–44
- Russ G (2002) Yet another review of marine reserves as reef fishery management tools. In: Sale PF (ed) *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, New York, pp 421–443
- Russ G, Alcalá AC (1998) Natural fishing experiments in marine reserves 1983–1993: role of life history and fishing intensity in family responses. *Coral Reefs* 17:399–416
- Sabatés A (1990) Distribution pattern of larval fish populations in the northwestern Mediterranean. *Mar Ecol Prog Ser* 59:75–82
- Sabatés A, Olivar MP (1996) Variation of larval fish distributions associated with variability in the location of a shelf-slope front. *Mar Ecol Prog Ser* 165:11–20
- Sale PF (1978) Coexistence of coral reef fishes—a lottery for living space. *Environ Biol Fish* 3:337–359
- Sale PF (1984) The structure of communities of fish on coral reefs and the merit of a hypothesis-testing manipulative approach to ecology. In: Strong DR Jr, Simberloff D, Abele LG, Thistle AB (eds) *Ecological communities: conceptual issues and the evidence*. Princeton University Press, Princeton, N.J., pp 478–490
- Sale PF (1998) Appropriate spatial scales for studies of reef-fish ecology. *Aust J Ecol* 23:202–208
- Samoilys M (1988) Abundance and species richness of coral reef fish on the Kenyan coast: the effects of protective management and fishing. *Proc 6th Int Coral Reef Symp*: 261–266
- Shulman GE, Love RM (1999) The biochemical ecology of marine fishes. In: Southward AJ, Tyler PA, Young CM (eds) *Advances in marine biology*. Academic Press, San Diego
- Spyker KA, Berghe EP van der (1995) Diurnal abundance patterns of Mediterranean fishes assessed on fixed transects by SCUBA divers. *Trans Am Fish Soc* 124:216–224
- Steele MA (1997) The relative importance of processes affecting recruitment of two temperate reef fishes. *Ecology* 78:129–145
- Thresher RE, Gunn JS (1986) Comparative analysis of visual census techniques for highly mobile, reef-associated piscivores (Carangidae). *Environ Biol Fish* 17:93–116
- Tziperman E, Malanotte-Rizzoli P (1991) The climatological seasonal circulation of the Mediterranean Sea. *J Mar Res* 49:411–434
- Underwood AJ (1990) Experiments in ecology and management: their logics, functions and interpretations. *Aust J Ecol* 15:365–389
- Underwood AJ (1997) *Experiments in ecology*. Cambridge University Press, Cambridge
- Underwood AJ, Chapman MG (1996) Scales of spatial pattern of distribution of intertidal invertebrates. *Oecologia* 107:212–224
- Valles H, Sponaugle S, Oxenford HA (2001) Larval supply to a marine reserve and adjacent fished area in the Soufrière Marine Management Area, St Lucia, West Indies. *J Fish Biol* 59 [Suppl. A]:152–177
- Vigliola L, Harmelin-Vivien M (2001) Post-settlement ontogeny in three Mediterranean reef fish species of the genus *Diplodus*. *Bull Mar Sci* 68: 271–286
- Vigliola L, Harmelin-Vivien ML, Biagi F, Galzin R, García-Rubies A, Harmelin J-G, Jouvenel JY, Le Diréac'h-Bousier L, Macpherson E, Tunesi L (1998) Spatial and temporal patterns of settlement among sparid fishes of the genus *Diplodus* in the northwestern Mediterranean. *Mar Ecol Prog Ser* 168:45–56
- Walsh WJ (1983) Stability of a coral reef fish community following a catastrophic storm. *Coral Reefs* 2:49–63
- Wantiez L, Thollot P, Kulbicki M (1997) Effects of marine reserves on coral reef fish communities from five islands in New Caledonia. *Coral Reefs* 16:215–224
- Watson M, Righton D, Austin T, Ormond R (1996) The effects of fishing on coral reef fish abundance and diversity. *J Mar Biol Assoc UK* 76:229–233
- Wiens JA (1989) Spatial scaling in ecology. *Funct Ecol* 3:385–397
- Williams DM (1991) Patterns and processes in the distribution of coral reef fishes. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, New York, pp 437–474
- Williams DM, Hatcher AI (1983) Structure of fish communities on outer slopes of inshore, mid-shelf and outer shelf reefs of the Great Barrier Reef. *Mar Ecol Prog Ser* 10:239–250