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Biomass Size Spectra in Littoral Fishes in Protected and Unprotected Areas in the NW Mediterranean

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The biomass size spectra in the littoral rocky fish communities in the Medes Island Marine Reserve and three unprotected localities from the NW Mediterranean were studied over a period of two years. A large number of individuals (81 478 in the protected area and 59 536 in the unprotected zones), belonging to 57 species, were censused. Communities were studied in different characteristic habitats (rocky bottoms and *Posidonia oceanica* sea grass beds). The slopes of the curves for the normalized size spectra showed that fish biomass in rocky areas was nearly constant from the smallest to the largest size classes. That trend was observed in both the unexploited and the moderately exploited areas, suggesting that the removal of large ichthyophagous individuals (e.g. *Dentex dentex*, *Dicentrarchus labrax*, *Epinephelus marginatus*) did not significantly affect the scale of population biomass with size. The pattern was different for the seagrass bed communities, in that the biomass of the larger size classes tended to increase in the protected area, whereas biomass was nearly constant across all the size classes in the exploited area. These results suggest that the communities at seagrass beds could be more sensitive to disturbance, because a large portion of the fish biomass is concentrated in one or a few species (e.g. *Sarpa salpa*). This study underscores the interest held out by marine reserves as a point of reference for studies on fish community size spectra and point out the existence of dissimilar size spectrum distributions in heterogeneous communities.

Keywords: biomass spectra; size spectra; littoral fishes; marine reserve; Mediterranean Sea

Introduction

The relationship between abundance and size distributions in a community is a fundamental aspect of population ecology that has been the subject of considerable work in recent decades (e.g. Margalef, 1974; Griffiths, 1998). In aquatic studies, one method commonly employed compares the density of all organisms belonging to the different size classes through what are called biomass size spectra. This method was first developed by Sheldon *et al.* (1972), who suggested that biomass follows uniform trends in the plankton (equal-biomass hypothesis), being considered as a promising approach to aquatic ecology (Dickie *et al.*, 1987).

Biomass size spectra make it possible to analyse the distribution of biomass in the different size groups making up a community and the effect of system productivity on that relationship (Sprules & Munawar, 1986). This method is normally related to energy use by organisms of different sizes (Platt & Denman, 1978; Thiebaux & Dickie, 1993), is valuable in comparing patterns among communities or habitats (e.g. Duplisea & Drgas, 1999) and in measuring the level of stress in a given area (e.g. Schwinghammer, 1988; Warwick & Clarke, 1996; González-Oreja & Saiz-Salinas, 1999). The results of these studies show that in the productive areas the biomass decreases with size, whereas in the less productive areas the biomass increases with size. A similar pattern can be observed in areas of high or low level of stress. Most studies have been performed on small organisms, mainly phytoplankton, zooplankton and meiofauna (Rodríguez & Mullin, 1986; Cattaneo, 1993; Rasmussen, 1993), being less common in larger organisms as fishes (Haedrich, 1986; Haedrich & Merret, 1992; Macpherson & Gordoa, 1996; Rice & Gislason, 1996). This low number of studies, some of them insufficiently replicated over space and time, has led to too much speculation regarding the patterns and, obviously, in the generality of the conclusions (Rodríguez, 1994). Furthermore, many size spectra have been constructed assigning to each species uniquely to one body size, without an accurate size distribution of each species in the system and thus avoiding a comparative approach

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between communities and areas (Duplisea & Drgas, 1999).

In fish communities anthropic alterations are very common (e.g. fishing) and may bring about significant disturbances in the relationship between size and abundance (Jennings & Kaiser, 1998). This means that the size distribution will be distorted to a greater or lesser extent and hence that it will be difficult to establish the natural relationship between abundance and body size and how that relationship may be conditioned by the different biotic and abiotic factors (e.g. habitat, productivity, fishing). An appropriate scenario for estimating fish biomass-size spectra relationships is one in which data can be compiled on a population under conditions in which the whole community is unexploited and all the factors affecting population structure are pristine or at least as natural and undisturbed as possible. Clearly, studies of populations or communities in the unexploited state can only be carried out in marine protected areas of sufficiently long standing to have allowed the ecosystem to recover to its original state (Marquet *et al.*, 1990; Jennings *et al*, 1995; Warwick & Clarke, 1996; Macpherson *et al.*, 2000).

The present paper analyses the biomass size spectra in the demersal fish community in the Medes Island Marine Reserve (NW Mediterranean, Spain). The reserve was established in 1983, and all fishing around the islands is prohibited. The length of time that has elapsed since the reserve's inception, its relative isolation and size of the reserve make this protected area an ideal site for studying fish populations in conditions that can be presumed to resemble the conditions that prevailed before the onset of intense fishing activity mostly in recent decades. The increase in the fishing activities was substantial in the Catalan coasts after the 1950s, where the total fish landings doubled previous values (Bas *et al.*, 1985). To have a more complete picture of the biomass spectral patterns in the different fish assemblages and their relationship to the effects of fishing, these same relationships were also studied at three exploited locations on the Costa Brava shoreline in the NW Mediterranean Sea. Considering that these studies may be complementary alternatives to population-based approaches, including fisheries management (Moloney & Field, 1985; Rice, 2000), the main objectives are to demonstrate the utility of marine reserves to know: (1) the fish biomass spectral patterns in areas from which man activities have been excluded, (2) the relationship of these patterns to habitat (rocky bottoms and *Posidonia* beds), and (3) the response of these biomass spectra to fishing activities.

Material and Methods

Study areas

The Medes Islands marine reserve is a small protected archipelago (*ca.* 300 ha) off the coast of NE Spain (Mediterranean Sea, 42°02′55″N, 3°13′30″E), consisting of seven islets and a few rocky reefs. The islands are rocky, with vertical walls and broken rocks covered by encrusting photophilic algae, except along the western side, where there is a *Posidonia oceanica* sea grass bed from a depth of 3–4 m to some 20 m. On most bottoms there is a muddy strip beginning at the 30 m isobath. Numerous studies have been carried out on the plant and animal communities present and on the changes taking place in such communities, as well as on the bottom structure and hydrographic features of the reserve (e.g. Zabala & Ballesteros, 1989; Sala & Boudouresque, 1997 and references cited therein). Four sites in the protected zone having the protected area's four different characteristic habitats, namely, gently sloping rocky bottoms (GSR), rocky bottoms with large broken rocks (BR), vertical walls (VW), and the *Posidonia oceanica* sea grass beds (PO), were chosen (Figure 1).

Three unprotected locations on rocky portions of the Costa Brava shoreline in the NW Mediterranean Sea were also sampled. The localities were l'Estartit (at a distance of one mile north of the Medes Islands Marine Reserve), Port de la Selva, and Tossa, each of these last two localities being roughly 50 km to the north and to the south of the Medes Islands Marine Reserve, respectively. The localities were chosen on the basis of morphological similarities between the bottoms and communities located there and those in the Medes Islands (Ros *et al.*, 1985; Zabala & Ballesteros, 1989). The bottoms sampled at l'Estartit and Tossa were rocky and gently sloping, with a strip of mud and sand starting at 30 m. At Port de la Selva the study site was a broad *Posidonia* bed down to 18–22 m, where the bottom turned to mud (Figure 1).

Fish communities

Fish assemblages in the protected and unprotected areas have been studied in detail by García-Rubies and Zabala (1990) and García-Rubies (1999). These studies, as well as other papers cited below, show that species can be clearly divided into two large species assemblages, one located in the rocky zones and the other on the sea grass beds.

Over 64 demersal fish species are taken in the study area (García-Rubies, 1999). In terms of number of species, the fish fauna of NW Mediterranean littoral

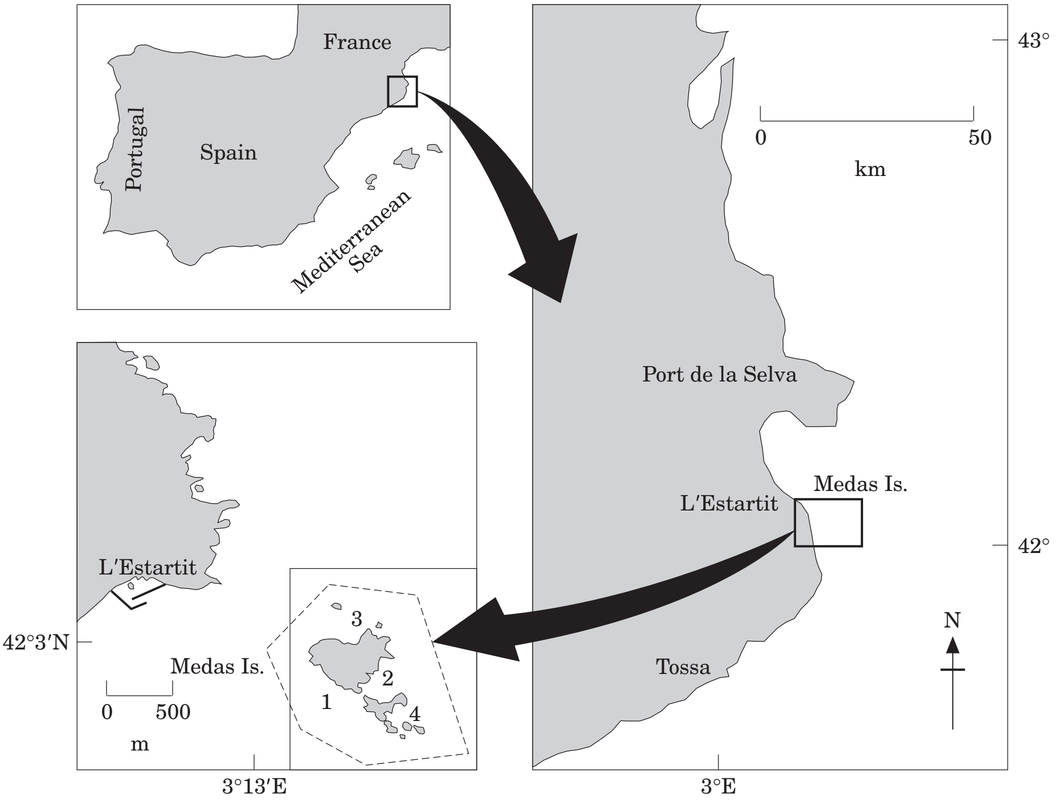

FIGURE 1. Location of the study sites (Port de la Selva, l'Estartit, Medas Islands and Tossa) along the northwestern Mediterranean coast. Arrows indicate study sites. Numbers in Medas Islands indicate sampling sites.

rocky areas is in large measure dominated by the Families Labridae, Sparidae, and Blenniidae, which account for more than 40% of the species observed, while many other families are represented by only a few species (Bell, 1983; Harmelin, 1987; García-Rubies, 1999). The *Posidonia oceanica* bed communities are less diverse than the rocky bottom communities (Harmelin-Vivien, 1983; Francour, 1994). Fish inhabiting the sea grass beds are generally small in size and more or less homochromatic or homotypic. The Families Labridae, Sparidae, Serranidae, and Scorpaenidae can account for up to 50–70% of the total fish biomass.

Census data

Fish censuses were carried out twice yearly, in autumn (November–December) 1997 and 1998 and in late spring–early summer (June–July) 1998 and 1999. Random transects measuring 5 × 200 m were censused at depths of 0, 10, 20, and 30 m at each of the seven sites (Vertical walls in the reserve was only censused twice). Blennies, gobiids and other small or cryptic species were sampled separately, following the same transect scheme, in order to obtain a more accurate estimation of their abundance levels and sizes. All transects were carried out in calm weather and high visibility conditions to minimize potential bias due to environmental conditions or visual accuracy. In any case, it should be borne in mind species (about seven) of the family Gobiesocidae (Hofrichter & Patzner, 2000) and species usually dwelling in caves or holes (e.g. *Muraena helena*, *Conger conger*, *Phycis phycis*) may be undersampled and they were excluded from the analysis.

Plastic tablets bearing the silhouettes and shapes of individuals of different sizes were used to minimize errors in estimating specimen size (Harmelin-Vivien *et al.*, 1985). All species were censused on all sampling dives. Two scuba divers performed all the censuses considered in this study, and the same diver always evaluated the same group of species in order to minimize possible error in the abundance counts and size estimates (see Macpherson *et al.*, 2000). Numbers of individuals and individual sizes were recorded on each dive. Fish size was estimated by 5 cm size class following the recommendations made by different researchers (e.g. Harmelin-Vivien *et al.*, 1985; St John *et al.*, 1990; Girolamo & Mazzoldi, 2001). Furthermore, in order to evaluate the potential differences between the real sizes and the size estimates recorded on the visual censuses, a validation experiment was held (see Macpherson *et al.*, 2000). Two divers estimated the sizes of previously captured specimens on the bottom, belonging to five common species (sparids and labrids) and ranging between 7 and 38 cm (TL). The differences between observers and the size estimates and the real size were tested using Kolmogorov-Smirnov tests. A *t*-test was used to verify differences on mean accuracy of size estimates between observers. The accuracy is considered as the ratio between real and observed values (St John *et al.*, 1990). The results of the size validation experiment indicated that there were no significant differences between real size and the size estimates made by either of the two divers (Kolmogorov–Smirnof two-sample test, $P<0{\cdot}001$), nor differences among observers. Mean accuracy of estimates was high (mean=1·017 and 1·014, std=0·064 and 0·066, for observers 1 and 2 respectively) and differences among observers were not significant (t=0·927; df=81; $P=0{\cdot}357$). These results are in agreement with previous papers (see above), suggesting that the use of 5 cm intervals have not a significant bias in size estimations.

The number of specimens and size frequencies were compiled for each species at each site. The size range was from 2 to 120 cm, with length units being converted to weight using available weight-length relationships (e.g. Gordoa *et al.*, 2000, and unpublished data).

Biomasses of fishes were aggregated within $\log_2$ size classes (in grams) regardless of taxa. Normalized biomass spectra (NBSs) was obtained by regressing the $\log_2$ of the biomass of each size class divided by the width of the respective size interval (dependent variable), against the upper limit of the correspondent size class (independent variable). This makes the biomass density size distribution independent of the size intervals, which allows to compare results from different communities, whatever the size of the organisms (see also Platt & Denman, 1978; Sprules & Manuwar, 1986; Blumenshine *et al.*, 2000). A slope equal to -1 indicates an even distribution of biomass over the size spectra; a slope steeper than -1 reflects a decrease in biomass with size, and a slope shallower than -1 indicates an increase in biomass with size. The regressions were performed separately for each sampling season and for each of the four sites in the protected zone and the three littoral localities in the unprotected areas for all four depth strata at each site combined.

The percentage of contribution to the total biomass by the different trophic groups was also calculated for each site and sample. Five trophic groupings were used (microphagous, mesophagous, herbivores, omnivores and ichthyophagous) following Bell and Harmelin-Vivien (1983) and Sala (unpublished data). A repeated measures ANOVA was used to test differences among sites in mean trophic grouping biomass. Original data were log-transformed to meet ANOVA's assumptions.

Results

Fifty-seven species (81 478 individuals in the protected area and 59 536 individuals in the unprotected zones) were recorded during the two years. The number of species recorded in the protected area by sampling season was higher at the rocky site (mean=49·4, SD=0·98) than at the *Posidonia* bed site (mean=33·5, SD=1·29) (Table 1). Certain medium and large species, which are highly vulnerable to fishing activity (e.g. *Sciaena umbra*, *Labrus viridis*, *Epinephelus marginatus*), were usually not present at the unprotected localities, hence the number of species at the rocky sites in the exploited localities (l'Estartit and Tossa) was lower (mean=39·8, SD=1·81) than in the protected area. On the other hand, no such difference was observed for the protected and unprotected *Posidonia* bed sites (mean=32·2, SD=0·96), where these highly vulnerable species were less common, even in the marine reserve (Table 2).

The results of the ANOVA showed significant differences between mean biomass of rocky sites for microphagous, omnivorous and ichthyophagous predators (Table 3). After the post-hoc SNK test, mean biomass of microphagous was higher in large broken rocks protected site; rocky sites inside protected area showed a significant higher biomass of ichthyophagous (e.g. *Dentex dentex*, *Epinephelus marginatus*) than in unprotected sites. By trophic grouping, most of the biomass at the rocky sites in the unexploited area consisted of omnivorous fishes and mesophagous predators (Figure 2). In the exploited areas, mesophagous predators made up a high proportion of the biomass. Omnivorous showed a significant lower biomass in l'Estartit site (unprotected gently slopping rock). In the *Posidonia* bed community, herbivores and mesophagous predators accounted for the largest share of the biomass, though predominance patterns differed in the unexploited and exploited areas. The protected *Posidonia* area showed higher biomass in all trophic groups, except for mesophagous group, than in non protected *Posidonia* area (Table 3). By percentages, herbivores contributed over half the total biomass in the reserve but less than a fourth of the total biomass in the unprotected areas (Figure 2).

Table 1. Biomass by species ($g\,1000\,m^{-2}$) in the different sites of the protected area. Values represent the average and standard deviation from the different transects carried out in each site (GSR=Gently sloping rock; LBR=Large broken rocks; VRW=Vertical rock walls and *Posidonia* bed). Different trophic groupings are also indicated (MI=microphagous predators; ME=mesophagous predators; H=herbivores; O=omnivores; and I=ichthyophagous predators)

		GSR		LBR		VRW		*Posidonia* bed	
		Mean	std	Mean	std	Mean	std	Mean	std
Blenniidae									
Aidablennius sphynx	MI							58·4	3·6
Coryphoblennius galerita	MI	15·6	2·6						
Lipophrys canevai	MI	48·2	7·9	65·6	3·7	67·8	3·8		
Lipophrys trigloides	MI	67·5	22·1	77·6	6·8	74·3	9·5		
Parablennius gattorugine	ME	110·0	51·7	226·1	39·6	139·6	19·8		
Parablennius incognitus	MI	390·5	35·2	452·8	34·3	527·8	11·5		
Parablennius pilicornis	MI	21·8	10·4			11·9	2·3	10·1	9·8
Parablennius rouxi	MI	662·3	24·2	271·7	28·7	386·8	8·7		
Parablennius sanguinolentus	MI							125·4	11·6
Parablennius tentacularis	MI	5·4	1·5					0·8	1·5
Parablennius zvonimiri	MI	10·0	1·8	11·3	2·4	13·4	1·5		
Gobiidae									
Gobius auratus	MI	136·6	1·8	25·3	4·6	66·0	10·9		
Gobius buchichi	MI	45·2	1·8	560·3	191·2			12·3	8·7
Gobius cobitis	ME							34·4	22·9
Gobius cruentatus	ME	14·4	4·6	14·0	3·0				
Gobius geniporus	MI	12·8	5·4	16·3	2·4			5·2	4·3
Labridae									
Coris julis	ME	11258·6	3089·2	12959·2	1·7	11108·1	3984·4	10013·2	1769·7
Ctenolabrus rupestris	MI	11·8	6·9	81·2	6·9	28·5	3·0		
Labrus bimaculatus	ME	1100·6	6·1	720·4	30·9				
Labrus merula	ME	2410·7	501·2	1943·2	32·6	2123·8	51·3	18095·5	1061·6
Labrus viridis	ME	811·4	44·9	142·9	2·7			2345·3	222·0
Symphodus cinereus	MI	15·9	0·9	81·1	2·7			256·6	44·8
Symphodus doderleini	ME	309·8	6·0	476·0	15·7	309·8	4·2	123·3	4·9
Symphodus mediterraneus	MI	2175·3	189·1	1080·3	4·2	2325·7	63·7	1147·5	34·3
Symphodus melanocercus	MI	600·7	11·1	608·9	8·5	628·0	33·8	581·8	0·7
Symphodus ocellatus	MI	279·9	25·4					1201·1	63·3
Symphodus roissali	MI	160·6	222·3	436·6	44·1	2593·8	301·7	468·5	166·8
Symphodus tinca	ME	29743·3	19918·3	86268·8	16186·4	36940·4	1957·2	282404·6	36584·7
Symphudus rostratus	MI							489·7	14·2
Thalassoma pavo	MI	227·1	12·7	679·8	6·5	167·5	4·1	198·8	10·5
Mugillidae									
Mugil spp.	MI	526·4	14·3	333·1	1·3			2184·6	538·5
Mullidae									
Mullus surmuletus	ME	1134·8	20·6	1740·8	187·1	1358·6	12·1	2974·5	33·4
Pomacentridae									
Chromis chromis	MI	19409·8	671·3	46687·5	3394·8	17513·2	3810·0	2904·0	51·2
Sciaenidae									
Sciaena umbra	ME	17789·9	6326·7	72843·6	9187·5				
Scorpaenidae									
Scorpaena porcus	ME							359·5	128·4
Scorpaena scrofa	ME	3033·4	257·5	688·7	23·7	2756·0	190·4		
Serranidae									
Anthias anthias	MI	11079·8	438·0	45582·2	1763·2	11126·2	565·1		
Dicentrarchus labrax	I			46515·4	2250·0				
Epinephelus marginatus	I	31520·7	986·9	281775·8	1289·7	68236·2	1325·1		
Serranus cabrilla	I	5210·6	621·9	4980·4	2556·8	5572·6	748·4	490·4	156·7
Serranus scriba	I							158·4	55·9
Sparidae									
Dentex dentex	I	622·0	28·7	38456·7	3847·6			3191·3	24·6
Diplodus annularis	O			533·1	86·5			4305·0	2039·7
Diplodus cervinus	ME	6795·8	3595·0	6635·2	1762·4	1697·8	73·6	944·7	629·8
Diplodus puntazzo	O	6979·2	3112·2	9996·2	313·7	8217·2	450·0	4049·2	2699·5
Diplodus sargus	O	113386·5	26844·3	110250·8	34078·8	126555·3	550·4	17362·7	2505·7
Diplodus vulgaris	O	14355·6	7783·9	9941·9	2599·5	9689·9	1637·1	1122·8	532·3
Lithognathus mormyrus	ME							2581·9	769·0
Pagrus pagrus	ME	1209·2	613·2	3865·5	1503·0			676·4	26·3
Sarpa salpa	H	5132·1	332·3	6757·7	173·3	2793·6	228·1	195492·7	10931·2
Sparus aurata	ME	17631·4	248·3	3507·8	1552·0				
Spondyliosoma cantharus	O	91·8	2·9	1867·6	1339·4	140·6	134·2	1212·3	55·3
Tripterygiidae									
Trypterygion delaisi	MI	25·4	4·5	19·4	5·4	12·8	2·6		
Trypterygion tripteronotus	MI	90·3	4·6	165·0	4·5	109·2	4·3	58·4	10·5

TABLE 2. Biomass by species (g 1000 m^{+2}) in the different unprotected areas. Values represent the average and standard deviation from the different transects carried out in each site (GSR=Gently sloping rock and *Posidonia* bed). Different trophic groupings are also indicated (MI=microphagous predators; ME=mesophagous predators; H=herbivores; O=omnivores; and I=ichthyophagous predators)

		Tossa (GSR)		l'Estartit (GSR)		Port (*Posidonia*)	
	Trophic group	Mean	std	Mean	std	Mean	std
Blenniidae							
Aidablennius sphynx	MI					60·6	4·6
Blennius ocellaris	MI	118·5	19·4				
Coryphoblennius galerita	MI			21·7	3·0	192·7	15·7
Lipophrys canevai	MI	14·9	0·9	142·0	11·3	85·0	7·1
Lipophrys trigloides	MI	1019·3	538·0	198·0	15·3	645·1	48·1
Parablennius gattorugine	ME	134·5	60·2	644·3	42·4		
Parablennius incognitus	MI	315·3	135·6	539·6	41·8	919·5	72·3
Parablennius pilicornis	MI	531·5	387·5			83·7	11·2
Parablennius rouxi	MI	232·8	86·8	228·9	18·9	85·9	7·3
Parablennius sanguinolentus	MI					932·0	98·5
Parablennius zvonimiri	MI			9·5	0·9		
Gobiidae							
Gobius auratus	MI			66·9	5·3	149·7	11·5
Gobius buchichi	MI					210·6	19·4
Gobius cobitis	ME					401·4	50·8
Gobius cruentatus	ME	177·8	338·7	4·1	0·9		
Gobius geniporus	MI	123·2	137·9			23·1	3·7
Labridae							
Coris julis	ME	6256·7	4346·5	7608·0	1642·4	4979·7	1872·4
Ctenolabrus rupestris	MI	6890·7	13574·6	89·3	9·5		
Labrus bimaculatus	ME	29·6	7·9	22·7	45·4		
Labrus merula	ME	1934·1	1106·8	312·6	192·1		
Labrus viridis	ME			643·4	148·3		
Symphodus cinereus	MI	236·0	46·3	19·4	4·9	199·8	15·6
Symphodus doderleini	ME	578·4	269·8	230·9	1·2	187·6	18·4
Symphodus mediterraneus	MI	1458·5	823·4	2093·0	34·1	462·0	31·6
Symphodus melanocercus	MI	811·1	11·8	539·1	7·4	280·4	5·1
Symphodus ocellatus	MI	327·6	18·1	598·7	29·7		
Symphodus roissali	MI	515·6	318·2	562·5	248·3	329·3	117·2
Symphodus tinca	ME	108391·6	71598·1	71372·2	733·8	54179·8	4411·6
Symphudus rostratus	MI	132·8	69·8	16·8	3·6	136·6	9·3
Thalassoma pavo	MI	37272·8	67799·1	79·6	8·7		
Mugillidae							
Mugil spp·	MI	417·3	282·1				
Mullidae							
Mullus surmuletus	ME	660·1	405·3	9330·1	749·6	769·2	14·1
Pomacentridae							
Chromis chromis	MI	19469·6	12995·6	24747·9	2215·2	4015·2	323·5
Scorpaenidae							
Scorpaena maderensis	ME	561·6	869·5				
Scorpaena porcus	ME					31·1	3·7
Scorpaena scrofa	ME	1405·8	880·1	827·9	62·4		
Serranidae							
Anthias anthias	MI	7504·5	358·4	9075·7	682·5		
Epinephelus marginatus	I	1078·5	2156·9	457·3	14·6	452·3	44·9
Serranus cabrilla	ME	2483·3	544·6	2013·7	287·4	1800·8	920·0
Serranus scriba	ME	507·5	826·9	33·8	49·2	49·0	10·7
Sparidae							
Dentex dentex	I	2186·5	4372·9	696·0	1391·9		
Diplodus annularis	O					930·7	123·9
Diplodus cervinus	ME	6916·1	10285·4	1357·3	1748·3		
Diplodus puntazzo	O	4600·9	5024·2	1427·7	1171·6		
Diplodus sargus	O	58626·6	17624·3	37895·8	6552·2	8173·0	2854·3
Diplodus vulgaris	O	23692·1	12803·8	12686·7	10945·5	1482·2	634·2
Pagrus pagrus	ME	276·6	553·2	545·9	1091·9	156·4	53·9
Sarpa salpa	H	36640·4	24452·9	94126·4	7497·8	24213·0	1977·6
Sparus aurata	ME	997·2	1994·3	219·6	439·2	177·2	13·6
Spondyliosoma cantharus	O	32·7	65·5	168·2	336·4		
Tripterygiidae							
Trypterygion delaisi	MI			21·8	4·6		
Trypterygion tripteronotus	MI	190·0	119·7	187·7	14·3	123·0	9·1

TABLE 3. Biomass for each trophic grouping, ANOVA and SNK post-hoc tests between sites for each trophic grouping. Sites: Protected area, Gently sloping rock (PGSR), Large broken rocks (PLBR), *Posidonia* bed (POS); Unprotected areas, Tossa gently slopping rock (TGSR), l'Estartit gently slopping rock (EGSR), Port *Posidonia* bed (UPOS). Trophic groupings: MI=microphagous predators; ME=mesophagous predators; H=herbivores; O=omnivores; and I=ichthyophagous predators. *$P<0.05$, **$P<0.01$, ***$P<0.001$

Biomasses

Trophic groupings		PGSR	PLBR	POS	EGSR	TGSR	UPOS	N
ME	Mean	98563·9	197012·7	63226·3	95166·6	131638·3	319249·0	4
	SD	28428·8	29436·7	6329·3	3029·8	66895·0	361448·3	
MI	Mean	35438·5	96478·5	8743·0	39216·2	74486·2	9383·7	4
SD	1174·9	3671·2	579·8	2838·4	77925·2	469·1		
H	Mean	5132·1	6757·7	24213·0	94126·4	36640·4	195492·7	4
	SD	332·3	173·3	1977·6	7497·8	24452·9	10931·2	
I	Mean	32142·7	366747·8	452·3	1153·3	3264·9	3681·6	4
	SD	977·7	2490·6	44·9	2306·5	6529·8	175·6	
O	Mean	134813·1	132589·7	10585·9	54810·6	86952·4	28996·8	4
	SD	22689·5	30716·0	2285·8	5134·6	32553·9	3123·4	
All groups	Mean	61218·1	159917·3	21444·1	56894·6	66596·4	111360·8	20
SD	SD	51218·1	124610·0	22989·5	36573·7	62913·5	193120·9	

ANOVA

	df Site	MS site	df Error	MS error	F	*P*	Post-hoc
Rocky bottoms							
ME	3	0·473	9	0·127	3·723	ns	
MI	3	0·815	9	0·179	4·549	*	PLBR>EGSR=PGSR=TGSR
H	3	7·190	9	3·072	2·340	ns	
I	3	120·704	9	6·713	17·981	***	PLBR=PGSR>EGSR=TGSR
O	3	0·718	9	0·041	17·630	***	EGSR<PLBR=PGSR=TGSR
Posidonia bed	df	MS	df Error	MS error	F	*P*	Post-hoc
ME	1	3·072	3	0·429	7·159	ns	
MI	1	0·010	3	0·001	19·824	*	POS>UPOS
H	1	8·736	3	0·009	1015·351	***	POS>UPOS
I	1	8·801	3	0·008	1106·303	***	POS>UPOS
O	1	2·079	3	0·045	46·122	**	POS>UPOS

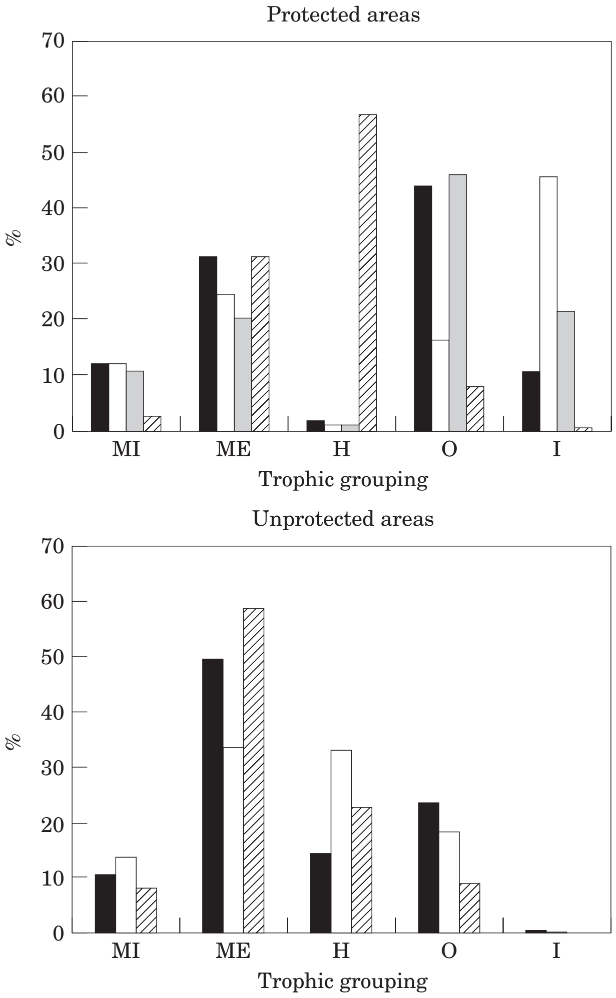

FIGURE 2. Mean percentage contribution by the different trophic groupings by site to the total biomass. Trophic groupings: MI=microphagous predators; ME=mesophagous predators; H=herbivores; O=omnivores; and I=ichthyophagous predators. Sites: Protected area, ■: Gently sloping rock (PGSR), □: Large broken rocks (PLBR), □: Vertical wall (VW), ▨: *Posidonia* bed (POS); Unprotected areas, ■: Tossa gently sloping rock (TGSR), □: l'Estartit gently sloping rock (EGSR), ▨: Port *Posidonia* bed (UPOS).

Table 4 sets out the results for the normalized size distributions for the different locations and sites by sampling season and year. In all cases the regressions explained a substantial proportion of the variance, and the R^2 values were mostly greater than 0·85 for the rocky bottoms; the values were somewhat lower (R^2=0·71–0·86) for the sea grass bed assemblage in the protected area.

The y-intercept values for the rocky sites were always higher than the values for the sea grass bed sites, indicative of an initially higher biomass at the rocky sites in both the protected and unprotected areas. The slopes for both the protected and unprotected rocky assemblages and the unprotected sea grass bed assemblage were not different to -1 in most cases, indicating that biomass tended to remain constant across the size classes. On the other hand, the slopes for the sea grass bed assemblage in the protected area were significantly less than -1, indicating that biomass tended to increase with size (Table 4). Differences between the protected area and the unprotected areas were only observed for the sea-grass bed communities, where the biomass values for the larger size classes in the unprotected areas were distinctly lower than in the protected area, clearly altering the slope for the size spectra (Figure 3).

Discussion

The results yielded by the biomass size spectra suggest that fish biomass in rocky areas is nearly constant from the smallest to the largest size classes. That trend was observed in both the unexploited and the moderately exploited areas. Furthermore, the biomass spectra were not significantly different for the three types of rocky bottoms considered, which suggests that the pattern observed may be representative for the most commonly found rocky substrata in the NW Mediterranean. The pattern was somewhat different for the seagrass bed communities, in that the biomass of the larger size classes tended to increase in the protected area, whereas biomass was nearly constant across all the size classes in the exploited area. This difference is attributable to a change in the composition of the food web in the community in the unprotected areas, resulting from the loss of an appreciable portion of herbivore biomass (consisting of large individuals of *Sarpa salpa*), which makes up more than half the total biomass in the unexploited area.

Differences in the slopes of the biomass size spectra have sometimes been associated with an area's productivity (Sprules & Munawar, 1986; Ahrens & Peters, 1991; Cyr & Peters, 1996), although that relationship has not always lent itself to easy interpretation, particularly when trying to compare benthic and pelagic systems (Sprules & Munawar, 1986; Rodríguez, 1994). Some workers have found higher slope values to be associated with areas of high productivity, where there is a higher concentration of biomass in smaller species with high turnover rates, while in more oligotrophic areas biomass is distributed evenly among the different size classes or may even increase for the larger size classes (Ahrens & Peters, 1991; Rasmussen, 1993; Saiz-Salinas & Ramos, 1999). This trend has been distinctly perceptible in fish communities, particularly when comparing

TABLE 4. Statistics for normalized biomass size spectra by area (protected and unprotected areas), locality (Medes Islands, Port de la Selva, l'Estartit, or Tossa) and season. Bottoms at the different sites were: gently sloping rocky bottoms, rocky bottoms with large broken rocks, vertical walls, and *Posidonia oceanica* sea grass beds. $P<0{\cdot}00001$ in all cases. Slopes different from −1 are indicated by an asterisk ($P<0{\cdot}05$)

	R^2	y-Intercept	SE	Slope	SE	*t*-test
Protected area						
Medes						
Gently sloping rock						
Autumn/Winter 1997	0·92	15·01	0·87	− 0·89	0·09	ns
Autumn/Winter 1998	0·90	14·80	0·90	− 0·87	0·09	ns
Spring/Summer 1998	0·92	14·99	0·86	− 0·89	0·09	ns
Spring/Summer 1999	0·97	14·80	0·53	− 0·91	0·05	ns
Vertical rock walls						
Spring/Summer 1998	0·89	15·10	1·11	− 0·99	0·11	ns
Autumn/Winter 1998	0·90	15·01	0·98	− 0·98	0·10	ns
Rock (large broken rocks)						
Autumn/Winter 1997	0·95	15·09	0·57	− 0·82	0·06	*
Autumn/Winter 1998	0·96	15·24	0·57	− 0·83	0·06	*
Spring/Summer 1998	0·95	15·02	0·57	− 0·82	0·06	*
Spring/Summer 1999	0·97	14·79	0·48	− 0·81	0·05	*
Posidonia bed						
Autumn/Winter 1997	0·73	12·38	1·24	− 0·57	0·12	*
Autumn/Winter 1998	0·71	12·16	1·27	− 0·55	0·13	*
Spring/Summer 1998	0·72	12·96	1·46	− 0·66	0·14	*
Spring/Summer 1999	0·86	9·94	0·39	− 0·23	0·04	*
Unprotected areas						
Tossa						
Gently sloping rock						
Autumn/Winter 1997	0·90	15·65	1·05	− 0·83	0·12	ns
Autumn/Winter 1998	0·90	15·10	0·96	− 0·96	0·11	ns
Spring/Summer 1998	0·89	16·09	1·16	− 1·03	0·13	ns
Spring/Summer 1999	0·89	15·78	1·09	− 1·00	0·12	ns
Port de la Selva						
Posidonia bed						
Autumn/Winter 1997	0·87	13·17	1·06	− 0·85	0·13	ns
Autumn/Winter 1998	0·86	13·75	1·04	− 0·82	0·12	ns
Spring/Summer 1998	0·86	13·30	1·18	− 0·91	0·14	ns
Spring/Summer 1999	0·91	12·72	0·81	− 0·81	0·09	ns
l'Estartit						
Gently sloping rock						
Autumn/Winter 1997	0·90	15·95	1·15	− 1·07	0·13	ns
Autumn/Winter 1998	0·91	15·46	1·06	− 1·03	0·12	ns
Spring/Summer 1998	0·89	15·82	1·15	− 1·05	0·13	ns
Spring/Summer 1999	0·91	15·71	1·02	− 1·03	0·11	ns

upwelling regions, which are highly eutrophic, with less productive abyssal zones (Macpherson & Gordoa, 1996). In the upwelling area, in which the abundance of small specimens was higher, the biomass clearly dropped off with increasing size and the community was dominated by mid-level predators, whereas in the less productive zone, where the biomass of small specimens was low, the biomass increased or tended to remain constant with size, being more abundant the apex predators (Macpherson & Gordoa, 1996).

The Medes Islands Marine Reserve is a typically oligotrophic system, though with higher benthic primary production at the rocky sites, where there is heavy algal cover, than in the *Posidonia* bed community (Ballesteros, 1989). In addition, biomass at the rocky sites consisted mainly of ichthyophagous and omnivorous species, while herbivores predominated at the *Posidonia* site. These differences may be associated with how energy is used in areas with different primary productions and differently structured food webs. The

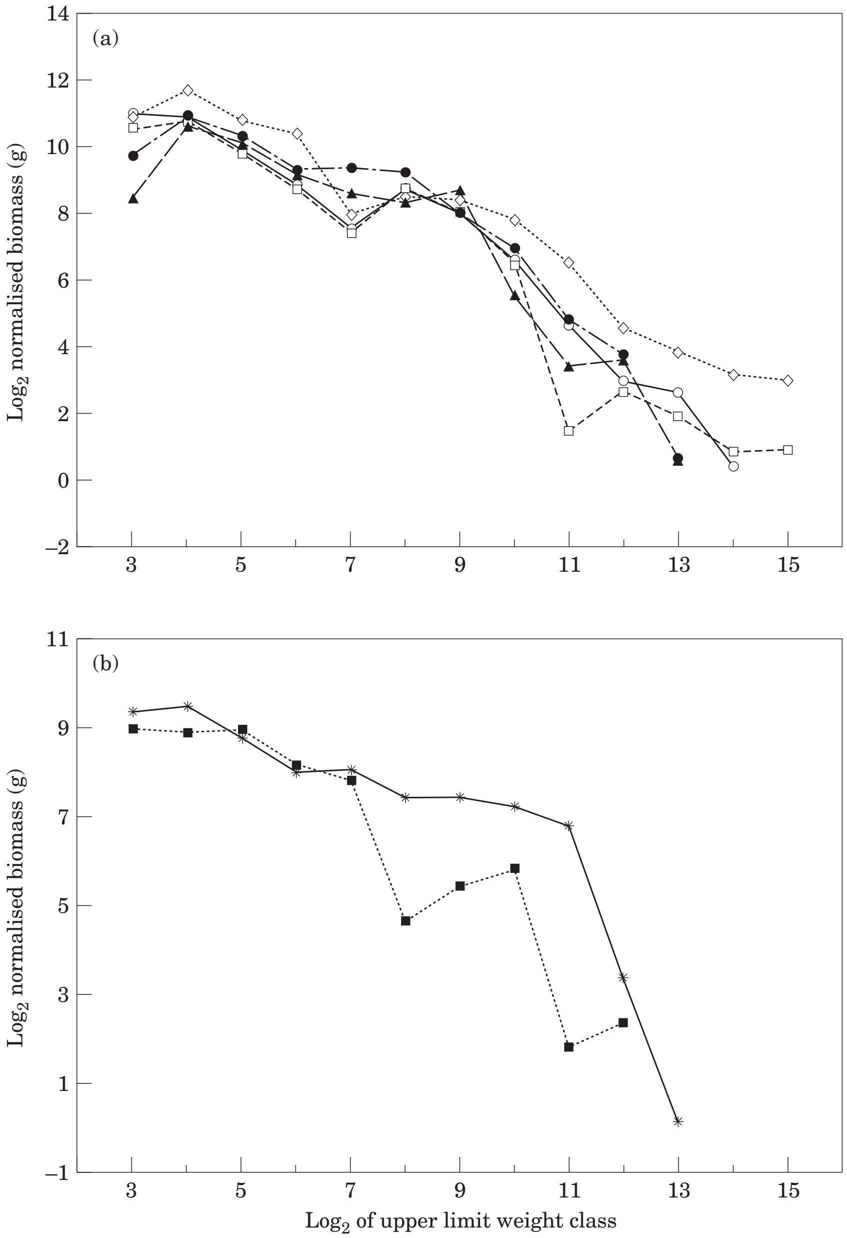

FIGURE 3. Plots of normalized biomass spectra of littoral fishes for the (a) rocky areas and (b) *Posidonia* bed areas in protected and unprotected areas in Spring–Summer 1998. Bottoms at the different rocky sites were: Protected area [gently sloping rocky bottoms (○), rocky bottoms with large broken rocks (◇) and vertical walls (□); Unprotected areas (Tossa (●) and l'Estartit (▲). Bottoms at the *Posidonia* beds were: Protected area (⋆) and unprotected area, Port de la Selva (■).

patterns observed for the *Posidonia* bed sites in the protected area were consistent with those reported for communities of large mammals in savannah habitats, where there are high herbivore density levels and biomass increases with body size (Silva & Downing, 1995). The results reported here are in agreement with the predictions of the ecological theory (Margalef, 1974; Hutchinson, 1978), suggesting a certain common pattern in the relationships between biomass distributions and productivity.

Although biomass distributions and abundance levels for the different trophic groupings are usually related to primary and/or secondary production, various researchers (e.g. Schmid *et al.*, 2000) have suggested that the distribution of body sizes may also reflect the physical structure of the habitat. This relationship is, however, not constant and several authors have showed that the benthic biomass size spectra of meiofauna and macrofauna in the northern and southern Baltic Sea tend to follow an irregular increase in biomass with size and not vary consistently among sediment types (Drgas *et al*, 1998; Duplisea & Drgas, 1999, see also Cattaneo, 1993). The availability and organization of habitat structure is very different at rocky sites than in sea grass beds, which affected the size distributions observed, because small species and/or small individuals were able to use habitats at the rocky sites that were not available in the *Posidonia* beds and hence were able to become more numerous (see also Rasmussen, 1993). Whether these same differences also exist in other regions with similar characteristics would be an interesting topic for future studies, and the findings would add to our understanding of the factors responsible for abundance-size-production relationships.

Studies relating biomass spectra in aquatic systems have been relatively common, but studies relating those same variables in undisturbed and disturbed areas have been less so. Certain researchers have reported scaling of population density according to body size not to be affected by changes in the processes that take place inside and outside marine reserves (Marquet *et al*., 1990). Jennings *et al*. (1995), comparing fish biomasses in unfished and fishing grounds, found that the biomass of non-target fish species doesn't change in response to the removal of their predators. Other studies comparing more or less disturbed areas have disclosed sharp changes in community size structure (Schwinghamer, 1988; Warwick & Clarke, 1996; González-Oreja & Saiz-Salinas, 1999; Blumenshine *et al*., 2000). Although, the ' reserve effect ' on the larger individuals of some fish species is well-known in the Mediterranean (García-Rubies & Zabala, 1990; Harmelin *et al*., 1995; Macpherson *et al*., 2000), the comparison of the communities inhabiting disturbed and undisturbed rocky sites did not display any differences with respect to global size spectra, suggesting that a system for offsetting densities like that observed by Marquet *et al*. (1990) or the existence of a complex diffuse predation (Hixon, 1991), could be in play. This would mean that some potentially determining factors affecting community structure, e.g. a moderate level of fishing effort (as in Tossa and l'Estartit) or the removal of large ichthyophagous individuals, are offset, such that they do not significantly affect scaling of population biomass with size. On the other hand, differences were observed for the sea grass bed sites, suggesting that the communities at those sites were more sensitive to disturbance, because a large part of the fish biomass is concentrated in one or just a few species, as has been reported for comparisons of the benthic and pelagic systems (Strayer, 1991).

The number of protected and unprotected localities studied was low, thus preventing the establishment of any definite conclusions as to patterns, but the results indicated that changes in the size spectra are only detectable when other scenarios are available for comparison (Marquet *et al*., 1990; Jennings *et al*., 1995). Consequently, one of the objects of the present paper is to underscore the interest held out by marine reserves as a point of reference for studies of this type (Bohnsack, 1993). Another result of this study is to show how ecosystems located close together spatially may have very different structures and present quite dissimilar size spectrum distributions (Strayer, 1991; Macpherson & Gordoa, 1996), suggesting that caution is in order when trying to establish general patterns encompassing heterogeneous communities.

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