Long-term and spillover effects of a marine protected area on an exploited fish community

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ABSTRACT: We assessed the development of the exploited fish community inside and around the Columbretes Islands Marine Reserve (CIMR), a marine protected area (MPA), 8 to 16 yr after fishing ceased in the reserve. Sampling was by annual lobster trammel net fishing, an experimental technique used inside the CIMR, and on-board commercial operations in adjacent fishing grounds. We examined trends in combined fish abundance and biomass (catch per unit effort), species richness and diversity, size structure, trophic level and species composition of the community. Our results showed the CIMR fish community continued to change throughout the study period as (1) abundance and biomass increased, (2) mean body size and trophic level increased and (3) species composition changed according to a linear model. Relative to nearby fished areas the CIMR fish community had (1) higher abundance and biomass, (2) lower species diversity and higher taxonomic distinctness, (3) larger relative body size and (4) no difference in mean trophic level. We found clear evidence of spillover of fish from the CIMR to the adjacent fishery as commercial fish yields at the MPA border (< 0.5 km from the boundary) increased continuously during the study period, despite being locally depleted due to fishing effort concentration (fishing the line). Furthermore, fish size and diversity at the border were intermediate between the CIMR and other fished zones, suggesting that this is a transitional zone influenced by this MPA. Our results show that changes in community abundance, biomass, size structure and species composition provide a clear and interpretable view of MPA recovery. Diversity indices are also useful; however, their interpretation is more difficult. We conclude that the creation of the CIMR has had a positive effect on the exploitable fish community and that there is evidence of exportation of biomass to the surrounding fishery. We highlight the advantage of using multiple community metrics to study changes in fish communities, yet recommend the need for caution when interpreting them.

KEY WORDS: Marine protected area · Fish community development · Spillover · Biomass · Diversity · Size spectra · Trophic level · Artisanal fishery · Mediterranean Sea

INTRODUCTION

Sustained exploitation of marine organisms has led to the depletion of populations of target species throughout the world (FAO 2007). One of the ecological costs of fishing is the incidental catch of organisms not targeted by the fisheries. In this context, artisanal fisheries are generally perceived as highly efficient low impact fisheries that generate few discards (e.g. Borges et al. 2001, Mas et al. 2004). However, despite

having preferred target species Mediterranean artisanal fisheries are multispecific and affect numerous species (Colloca et al. 2004, Goñi et al. 2008). Trammel nets are among the most important gears that artisanal fishers use in the Mediterranean Sea (e.g. Goñi et al. 2008). While trammel nets are often target specific, an important part of the catch consists of multi-species bycatch (Stergiou et al. 2006), as occurs in the spiny lobster *Palinurus elephas* trammel net fishery that operates throughout the western Mediterranean Sea

(Goñi & Latrouite 2005). The commercial bycatch of the western Mediterranean lobster fishery is made up of up to 87 commercial species of finfish, molluscs and crustaceans that are increasingly relied upon to supplement dwindling lobster yields (Quetglas et al. 2004). About 54% of the catch in number (excluding non-commercial benthos such as bryozoans, sponges, algae and echinoderms) are commercialised fishes of high value such as largescale scorpionfish *Scorpaena scrofa*, anglers *Lophius* spp., john dory *Zeus faber* and great forkbeard *Phycis phycis.*

Marine protected areas (MPAs) have become a popular management tool in the Mediterranean Sea with the last census reporting 66 operational areas in the western Mediterranean (Ramos-Esplá et al. 2004). Expected benefits of MPAs to fishes in this region include an increase in abundance, biomass and fecundity, as well as a potential for benefits to biodiversity (García-Charton et al. 2008). Indeed, high exploitation rates and limited mobility of species targeted by artisanal fisheries have resulted in rapid biomass build up inside western Mediterranean MPAs (Sánchez-Lizaso et al. 2000). The Columbretes Islands Marine Reserve (CIMR), was created in 1990 to, amongst broader fishery and conservation objectives, protect traditional *Palinurus elephas* fishing grounds. At that time all professional fishing was banned in the CIMR, though recreational fishing continued until 2002 when anchoring was prohibited and essentially drew closure on this activity. Studies conducted in the CIMR to assess its effectiveness on the lobster population, 7 to 12 yr after this MPA was established, showed that abundance and reproductive potential within the reserve was greater than in comparable fished areas (Goñi et al. 2001, 2003a), and that spillover of lobsters from the CIMR increased catches in the adjacent commercial fishery up to 1.5 km from its boundaries (Goñi et al. 2006). The CIMR also protects a diverse fish population, which in 1996, 6 yrs after protection was initiated, showed higher abundance and biomass than in equivalent fished areas (García-Charton et al. 2004). A study conducted between 1998 and 2000 on *Scorpaena scrofa* in the CIMR also showed that within the protected area individuals of this species were larger and more abundant (Reñones et al. 2001).

Most multispecies studies of MPA effects in the Mediterranean Sea have targeted shallow littoral fish communities assessed by underwater visual census (e.g. García-Charton et al. 2004, Harmelin-Vivien et al. 2008), while few studies have assessed the temporal changes of exploited communities in deep water using other methods (e.g. Goñi et al. 2001, Reñones et al. 2001). In this study we assess the development of the fish assemblage (hereafter 'community') exploited by the spiny lobster trammel net fishery 8 to 16 yr (1998 to

2006) after it was banned in 1990 in the CIMR. The distinctive characteristics of that community in the CIMR and in the nearby fished grounds at increasing distances from the CIMR are also explored. We have assumed that fishing effort in the nearby lobster fishery has remained constant during the study period (R. Goñi unpubl. data) and are certain that the fishing prohibition is well enforced in the CIMR. Therefore, we expect that abundance and biomass of fish species with high catchability in lobster trammel nets should follow increasing trends inside the CIMR while they should remain stable at lower levels in fished areas. Consequently we have hypothesized that (1) protection in the CIMR will mostly result in positive changes at the community level over time, (2) the fish community protected from lobster trammel net fishing in the CIMR will be different from that in comparable, nearby fished areas and (3) this difference will increase with distance from the CIMR boundary (or that, due to 'spillover' effects, the community in the fished areas closest to the CIMR will resemble the CIMR more than those farther away). To assess the change of the exploited fish community in the CIMR we examined trends in (1) total species abundance and biomass, (2) species richness and diversity, (3) community size structure and mean trophic level and (4) species composition. These variables were also used to compare the fish community in the CIMR with those in exploited areas at increasing distances from the CIMR boundary. Because the effects on diversity remain unclear, we have used a suite of indices to assess this response to fishing (Rochet & Trenkel 2003).

MATERIALS AND METHODS

Study site. This study took place in the CIMR and surrounding fishing grounds (Fig. 1). The CIMR is located 50 km east from the Mediterranean coast of Spain and protects 44 km^2 of volcanic rock and coralligenous habitats (maërl beds) with patches of gravel, sand and mud that extend down to depths of 80 m. Fishing grounds near the CIMR consist of patches of rock and maërl over expanses of gravel, sand and mud predominantly at depths of 60 to 100 m. The CIMR was a traditional lobster fishing ground before it was closed to fishing in 1990. Since then, fishing effort in the region has been concentrated along the CIMR boundaries and in nearby fishing grounds (<30 km from the CIMR) and the number of boats participating in the local lobster fishery has declined, while fishing effort per boat has steadily increased. During the study period, no more than 6 artisanal boats fished consistently in the area. There is also frequent bottom trawling near the CIMR although both fisheries rarely over-

lap. The MPA legislation prohibits all fishing except very limited recreational (prior to 2002 recreational fishing was allowed) and commercial fishing (pelagic species), which essentially renders the entire CIMR a 'no take zone'. Fishing regulations in the CIMR are well enforced by a permanent ranger staff.

Data collection. *CIMR:* Data were collected in experimental fishing surveys conducted annually between June and September inside the CIMR as part of a monitoring programme started in 1998. The surveys were carried out with one of the commercial boats that operate in the area, and with the same gear type used in the commercial fishery. A detailed description of the survey method is given in Goñi et al. (2003b). Surveys available for this study were for the 1998 to 2006 period and followed a standardized depth-stratified sampling design with approximately 9 randomly placed fishing sets in each of 2 depth strata: shallow (25 to 50 m) and deep (50 to 80 m). In total 163 fishing sets were available to study the development of the exploited community in the CIMR.

Fished areas: Fishery data were collected by means of sampling on board commercial lobster boats operating around the CIMR from 1998 to 2006 (except 2004) during the 6 mo (March to August) lobster fishing season. Whenever possible, sampling took place during 1 wk per month on board one of the boats that fished more consistently in the region. The observer sampled all the fishing sets that were carried out in that week without directing where fishing sets should be allocated. In this fishery, trammel nets (gear description in Goñi et al. 2003b) are set over rocky and coralligenous habitats and left in place (soaked) for several days (mean 4 to 5 d) depending on weather conditions. Over the study period 349 commercial fishing sets were sampled within 27 km of the CIMR boundary at depths of 50 to 100 m.

In all the commercial and experimental fishing operations, data on net length, soak time, fishing location and depth along with catch by species and individual size of all fish were recorded. All commercial species of fish caught, with the exception of pelagic species caught accidentally, were used in the analyses. Data for this study included 51 commercial fish species belonging to 20 families (Table 1).

Study design. *Community development within the CIMR:* To study the development of the fish community in the CIMR we used data collected in experimental surveys during the study period over the whole depth range (20 to 80 m) of the CIMR.

Spatial comparison of protected versus exploited communities: For the purpose of comparing the fish community protected in the CIMR with those in the nearby exploited areas, we grouped the data into 4 spatial categories (zones) according to distance from

each fishing set to the CIMR as follows: (1) within the CIMR, (2) fishing grounds bordering the CIMR within 0.5 km from its boundary or 'border grounds' (BOR), (3) fishing grounds located from 0.5 to 5 km from the
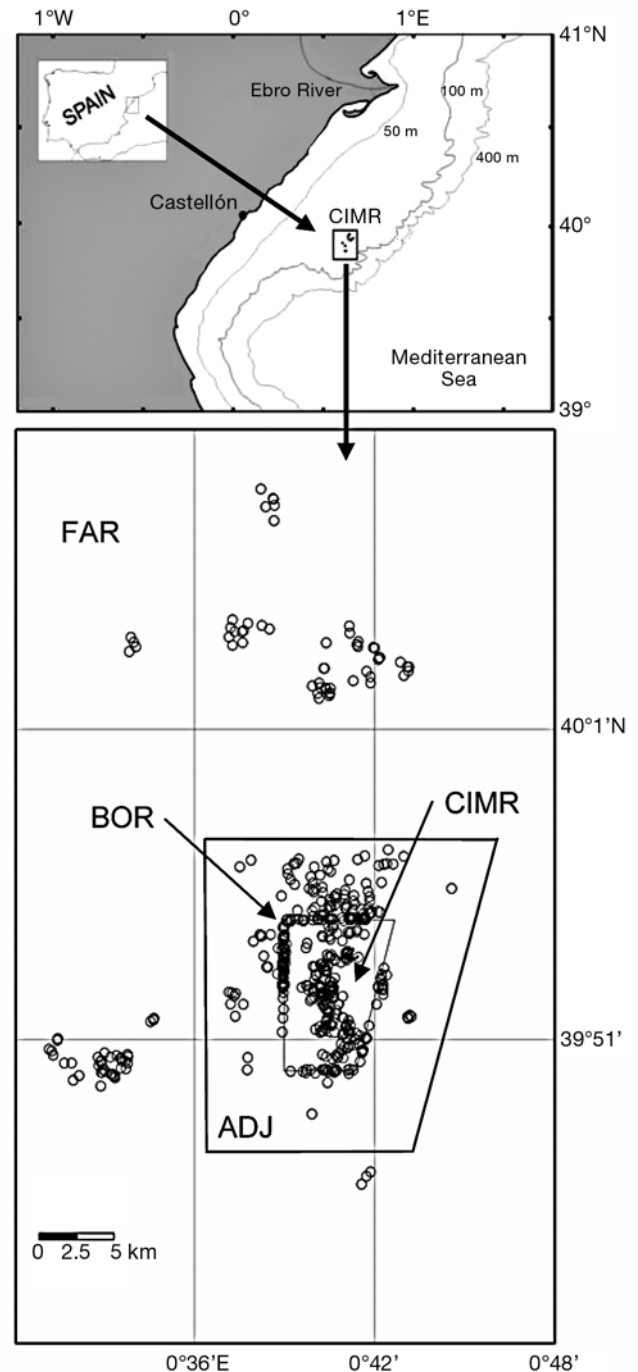

Fig. 1. The western Mediterranean Sea with the location of the Columbretes Islands Marine Reserve (CIMR) and surrounding fishing grounds showing the position of the fishing sets and zone designation. FAR: far grounds; BOR: border grounds; ADJ: adjacent grounds

Table 1. Species and mean abundance (catch per unit effort numbers, NCPUE, in no. fish per 600 m net) making up the fish community studied inside the Columbretes Islands Marine Reserve (CIMR) (n = 163 fishing sets) and the nearby fishery area (grouped as border, adjacent and far fished grounds, n = 349 fishing sets). –: no fish caught

| Family | Species | NCPUE | |
		CIMR	Fished zones
Scorpaenidae	*Scorpaena scrofa*	4.006	1.413
Rajidae	*Raja montagui*	2.809	0.164
Phycidae	*Phycis phycis*	1.145	0.466
Zeidae	*Zeus faber*	1.079	0.568
Sciaenidae	*Sciaena umbra*	0.712	0.251
Sparidae	*Dentex dentex*	0.461	0.103
Scyliorhinidae	*Scyliorhinus stellaris*	0.455	0.061
Rajidae	*Raja polystigma*	0.400	0.000
Lophiidae	*Lophius piscatorius*	0.361	0.728
Rajidae	*Raja brachyura*	0.326	–
Sparidae	*Spondyliosoma cantharus*	0.291	0.103
Sparidae	*Pagellus acarne*	0.227	0.224
Sparidae	*Pagellus erythrinus*	0.221	0.276
Torpedinidae	*Torpedo marmorata*	0.220	0.133
Sparidae	*Pagrus pagrus*	0.200	0.080
Lophiidae	*Lophius budegassa*	0.137	0.291
Uranoscopidae	*Uranoscopus scaber*	0.108	0.116
Serranidae	*Epinephelus marginatus*	0.052	0.012
Carangidae	*Trachurus picturatus*	0.050	0.015
Scyliorhinidae	*Scyliorhinus canicula*	0.041	0.110
Trachinidae	*Trachinus radiatus*	0.037	0.009
Triglidae	*Trigloporus lastoviza*	0.027	0.009
Congridae	*Conger conger*	0.021	0.020
Labridae	*Labrus bimaculatus*	0.020	0.018
Labridae	*Labrus merula*	0.020	–
Scorpaenidae	*Scorpaena porcus*	0.018	0.003
Serranidae	*Serranus cabrilla*	0.015	0.119
Carangidae	*Trachurus mediterraneus*	0.015	0.023
Sciaenidae	*Umbrina cirrosa*	0.015	0.014
Myliobatidae	*Myliobatis aquila*	0.013	–
Dasyatidae	*Dasyatis pastinaca*	0.012	0.006
Mullidae	*Mullus surmuletus*	0.012	0.087
Triglidae	*Aspitrigla obscura*	0.007	–
Merlucciidae	*Merluccius merluccius*	0.007	0.148
Carangidae	*Trachurus trachurus*	0.007	0.006
Sparidae	*Sarpa salpa*	0.006	0.000
Sparidae	*Sparus aurata*	0.006	0.009
Trachinidae	*Trachinus draco*	0.006	–
Sparidae	*Diplodus vulgaris*	–	0.017
Triglidae	*Lepidotrigla cavillone*	–	0.009
Sparidae	*Pagellus bogaraveo*	–	0.042
Phycidae	*Phycis blennoides*	–	0.010
Rajidae	*Raja asterias*	–	0.045
Rajidae	*Raja clavata*	–	0.003
Rajidae	*Raja radula*	–	0.003
Scorpaenidae	*Scorpaena notata*	–	0.006
Labridae	*Symphodus tinca*	–	0.006
Triglidae	*Trigla lucerna*	–	0.028
Triglidae	*Trigla lyra*	–	0.003
Gadidae	*Trisopterus luscus*	–	0.003
Gadidae	*Trisopterus minutus*	–	0.026
Total		**13.57**	**5.785**

CIMR boundary or 'adjacent grounds' (ADJ), and (4) fishing grounds located beyond 5 km from the CIMR boundary or 'far grounds' (FAR) (Fig. 1). For each spatial category we combined the samples from the whole study period. As we detected changes in abundance, biomass and diversity within the CIMR during the study period (see results on CIMR temporal change), one could object that combining data from the CIMR over the whole study period for comparisons with exploited zones may not be appropriate. However, we argue that by combining data the estimates of CIMR values will become more conservative and, thus, not hinder the interpretation of any community differences we have detected between the CIMR and fished zones.

Other obvious problems exist with a study of this kind. Firstly, only one marine protected area has been studied, so that the 'treatment' has not been replicated. Strictly speaking, samples taken within the CIMR for comparison with other locations are 'pseudoreplicates' (Hurlbert 1984). However, because the samples outside the CIMR are from similar nearby habitats (lobster fishing grounds) and they extend away from the CIMR in all directions (Fig. 1), at least partially mitigate this problem. Secondly, the sampling stations within the CIMR are, on average, closer to shallow water than those outside it, so that differences in species abundance, composition or diversity could result from habitat effects associated with shallow water environments. However, as described below, this was tested using 2-way significance tests (zone/distance from shallow water) and found not to be a problem. Prior to this, we did find that community composition at depths shallower than 50 m was different from that at greater depths, and therefore only CIMR samples from the deep stratum (>50 m) were used in the comparisons of the CIMR with fished zones.

Community development in exploited areas and spillover effects: To assess potential spillover effects of the CIMR on the adjoining fishery we examined the development of the fish community in each of the 3 exploited spatial categories described above using onboard fishery data.

Data analysis. *Abundance and biomass:* Abundance and biomass indices for the combined species were estimated by the catch per unit effort (CPUE) expressed in numbers (NCPUE) and weight (kg) (WCPUE) per 600 m of trammel net (standard length of experimental and commercial lobster trammel net fishing sets). The changes in abundance and biomass in the CIMR were tested using linear regression analyses of $\log_{10}(NCPUE + 1)$ and $\log_{10}(WCPUE + 1)$ as functions of time. One-way between-groups ANOVA was used to test for differences in $\log_{10}(NCPUE + 1)$ and square-root transformed (WCPUE) in the CIMR and the fished

zones. Homogeneity of variances was tested using Levene's test. Post-hoc comparisons were made using Tukey's honestly significant differences (HSD) test.

Diversity: To study the changes in species diversity, and to compare them between unfished and fished zones in each of the 9 yr studied, we used the following indices:

(1) Margalef's richness index (Margalef 1968):

$$d = (S - 1)/(\log_e N),$$

where S is the total number of species and N is the total number of individuals in the sample. As Margalef's index, d, is affected by the number of samples, for the spatial comparison we balanced sample size (number of fishing sets) between zones by removing randomly selected hauls as necessary.

(2) Simpson's evenness (dominance) index (Simpson 1949):

$$1 - \lambda = 1 - [\Sigma_i N_i (N_i - 1)]/[N(N - 1)],$$

where N_i is the number of individuals of the ith species in the sample.

We also calculated the diversity indices Δ^* and $\Delta+$ based on taxonomic distinctness (Warwick & Clarke 2001). We have focused on average taxonomic distinctness measures Δ^* and $\Delta+$, since average taxonomic diversity (Δ) has been shown in many studies (as it did in this one) to track species diversity measures such as Simpson's index quite closely. Thus, to remove the dominating effect of the species abundance distribution (x_i), leaving a measure that is more nearly a pure reflection of the taxonomic hierarchy, Δ is divided by the Simpson's index, to give average taxonomic distinctness:

$$\Delta^* = (\Sigma\Sigma_{i<j} \omega_{ij} x_i x_j)/(\Sigma\Sigma_{i<j} x_i x_j)$$

Another form of the taxonomic distinctness index takes the special case where quantitative data are not available and the sample consists simply of a species list (presence/absence data). In this case, both Δ and Δ^* reduce to the same coefficient:

$$\Delta+ = (\Sigma\Sigma_{i<j} \omega_{ij})/[S(S - 1)/2]$$

where S is the observed number of species in the sample and the double summation ranges over all pairs i and j of these species ($i < j$). The average taxonomic distinctness, $\Delta+$, of a species list is the average taxonomic distance apart from all its pairs of species. Thus $\Delta+$ is an intuitive definition of biodiversity, as average taxonomic breadth of a sample. All the richness and diversity indices were calculated using only fishing sets in which the number of species present was in excess of 5, as plots of indices calculated using fewer species tend to give unreliable results (R. Warwick & B. Stobart pers. obs.).

Size structure: To study the development of fish size in the CIMR and compare it across spatial categories we used a method based on the combined size structure of the 33 most abundant fishes, captured over time within the CIMR, and for all years combined across zones. This method has the advantage of allowing comparison of sizes of all species together, rather than individually, as is usually the case, and involves standardising the size of all individuals of each species with more than 2 individuals in the sample to a percentage of the maximum species-specific registered size (the maximum size of each species recorded, considering samples from all zones). For convenience, we refer to the percentage output as 'relative body size.' While this does not relate the sizes to the maximum attainable size for each species, e.g. those given in FishBase (available at www.fishbase.org), it removes the need to use size data that may have origins in other areas where fish maximum sizes can be very different from those attainable locally. The development of the size structure within the CIMR was explored using linear regression of the annual mean relative body size. The significance of the inter-annual slope was tested by ANOVA of the arcsine transformed percentages.

The size structure of the community in the CIMR (deep stratum only) was then compared with that of the fished zones by constructing size frequency distributions for each zone with all years combined and with each data set standardised to the zone total to eliminate differences in sample size. Resulting frequency distributions for zones were compared using nonparametric Kolmogorov-Smirnov tests. For species with sufficient number of individuals, change in body size over time was studied by linear regression analysis.

Trophic level: Mean community trophic level was calculated using data of the 51 fish species based on trophic categories obtained from Fishbase and Konstantinos & Vasiliki (2002). Changes in mean trophic level over time in the CIMR and the fished zones were explored using linear regression analysis while interzone differences were assessed using the nonparametric Kruskal-Wallis test.

Species composition: To examine differences in community species composition over time within the CIMR and between spatial categories, we used nonmetric multidimensional scaling ordination (MDS) with square-root transformed species abundance or biomass and the Bray-Curtis measure of similarity between samples. Temporal change of the communities in the different zones was tested by comparing yearly average points on an MDS to a linear sequence or seriation (e.g. see Clarke et al. 1993 for full explanation of the test). We used SIMPER analysis in PRIMER v. 6 to identify those species contribut-
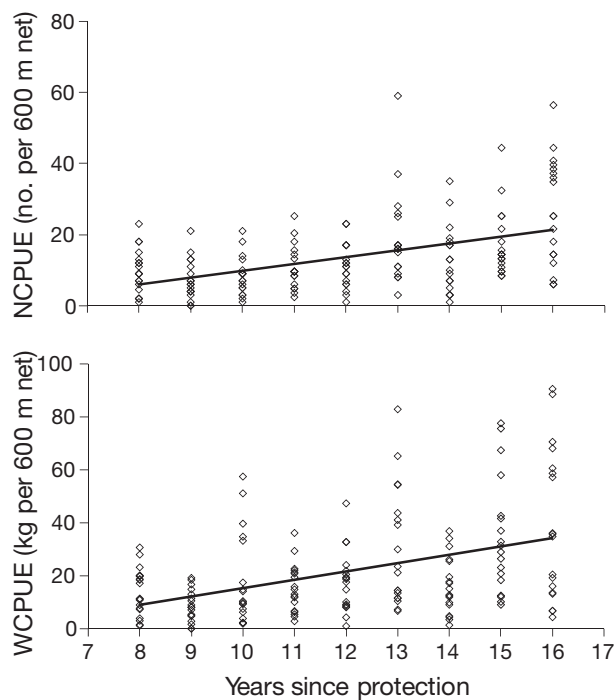
Fig. 2. Abundance (catch per unit effort in numbers, NCPUE) and biomass (catch per unit effort in weight, WCPUE) of the fish community within the CIMR as function of time (years)

ing to the dissimilarity between years within the CIMR, and the BVSTEP routine to determine which were the main species driving the temporal change. Two-way analysis of similarities (ANOSIM) was used to test for the degree of dissimilarity between zones across the different years, across sampling months (since the time of fishing varied from year to year among zones) and in relation to distance from shallow water. For the latter, distance to the nearest 40 m depth contour was divided into 4 categories: <1 km, 1–5 km, 5–15 km and 15–30 km. Two-way SIMPER was used to identify those species responsible for characterising each zone, and contributing to the dissimilarity between zones, across the 9 yr. Variability among samples within each zone was compared using the PRIMER routine MVDISP, which gives a value for relative multivariate variability within each group, as increased variability among samples has been regarded as a multivariate symptom of stress in marine communities (Warwick & Clarke 1993). The degree to which community development within the CIMR corresponds with a linear sequence was tested using the PRIMER routine RELATE. The multivariate techniques used are described fully by Clarke & Warwick (2001) and have been implemented using PRIMER v. 6 (Clarke & Gorley 2006).

RESULTS

Community change within the CIMR

Linear trends in univariate measures of the exploited fish community within the CIMR (Fig. 2, Table 2) indicated significant increases over time in both abundance and biomass. Slopes of regression analysis of species diversity in terms of richness (Margalef's d) and evenness (Simpson's $1-\lambda$) as a function of time were positive though not significant. In contrast, both taxonomic distinctness indices, Δ^* and $\Delta+$, showed significant decreases during the study period (Table 2), though the decrease was driven by *Mullus surmuletus*, a single representative of the family Mullidae, present only in the early years. Removal of this species from the analyses led to a non-significant decreasing trend.

Fish relative body size in the CIMR (mean of 33 fish species selected) increased significantly with time ($R^2 = 0.009$, $F_{1,2504} = 22.9$, p < 0.001) (Fig. 3). Relative mean fish sizes in the years 2004 and 2005 were particularly large, while in 2006 mean size was low. For 2004 this anomaly was caused by catches of unusually large individuals of *Raja brachyura*, while variation in 2005

Table 2. Results of linear regression analyses of log abundance (NCPUE + 1) (LogN), log biomass (WCPUE + 1) (Log Biom) and richness and diversity indices as a function of years of protection of the exploited fish community in the CIMR (20 to 100 m depth). Significant p-values are in **bold**

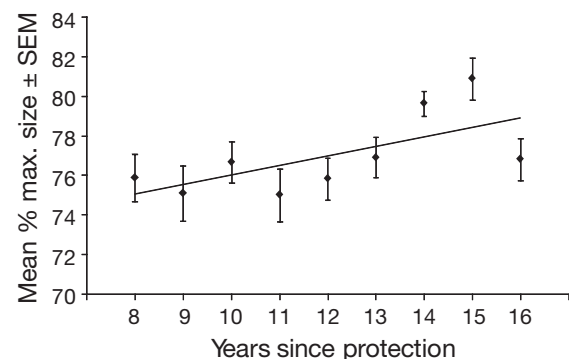| Factor	n	R^2	Slope b	t-statistic	p-value
LogN	163	0.218	0.057	6.423	**<0.001**
LogBiom	163	0.183	0.062	5.752	**<0.001**
Margalef's d	71	0.031	0.037	1.505	0.137
Simpson's $1-\lambda'$	71	0.009	0.004	0.798	0.428
Δ^*	71	0.065	−0.729	−2.197	**0.031**
$\Delta+$	71	0.064	−0.471	−2.175	**0.033**

Fig. 3. Mean percentage of maximum size ± SE of the mean (SEM) as a function of time (years) since protection for the 33 most abundant fish species sampled inside the CIMR

and 2006 was general and not attributable to a single species. Only 8 fish species were caught in sufficient numbers to analyse change in body size over time on an individual basis. Of these, *Scorpaena scrofa* ($R^2 = 0.028$, $F_{1,610} = 17.95$, p < 0.001), *Pagellus erythrinus* ($R^2 = 0.138$, $F_{1,34} = 6.48$, p = 0.02), *Phycis phycis* ($R^2 = 0.061$, $F_{1,178} = 11.7$, p < 0.001) and *Sciaena umbra* ($R^2 = 0.037$, $F_{1,110} = 4.24$, p = 0.04) significantly increased in size over time, while *Scyliorhinus stellaris* ($R^2 = 0.071$, $F_{1,68} = 5.20$, p = 0.03) decreased. Trends for the remaining 3 species, while not significant, suggested that *Dentex dentex* may be increasing in size ($R^2 = 0.013$, $F_{1,69} = 0.95$, p = 0.33) while sizes of *Lophius piscatorious* ($R^2 = 0.022$, $F_{1,59} = 1.35$, p = 0.25) and *Zeus faber* ($R^2 = 0.008$, $F_{1,173} = 1.49$, p = 0.22) may be decreasing.

Mean trophic level of the community within the CIMR increased over time, though the trend was slightly below the significant threshold ($R^2 = 0.02$, $F_{1,105} = 3.57$, p = 0.062). MDS plots for all samples averaged in each year (not shown) indicated significant linear trends (seriation) over time in fish species composition, both in terms of abundance and biomass (p < 0.02

in all cases). BVSTEP analysis revealed that *Lophius budegassa*, *L. piscatorius*, *Phycis phycis*, *Raja montagui*, *R. polystigma*, *Scorpaena scrofa*, *Scyliorhinus stellaris* and *Zeus faber* correlated at the 95 % level with the pattern produced, and are therefore the species driving the change. There were no significant results for seriation outside the CIMR (not shown), although the BOR area was almost significant ($\rho = 0.272$, p = 0.086), while the ADJ and FAR areas were not ($\rho = 0.005$, p = 0.46 and $\rho = 0.048$, p = 0.41 respectively).

Comparison between the CIMR and fished areas and spillover effects

Mean abundance and biomass of the fish community pooled for the entire study period differed significantly between zones (abundance $F_{3,433} = 14.35$, p < 0.001, biomass $F_{3,433} = 20.79$, p < 0.001) (Fig. 4). Post-hoc comparisons indicated that abundance was significantly higher inside the CIMR (mean ± SD NCPUE = 10.4 ±
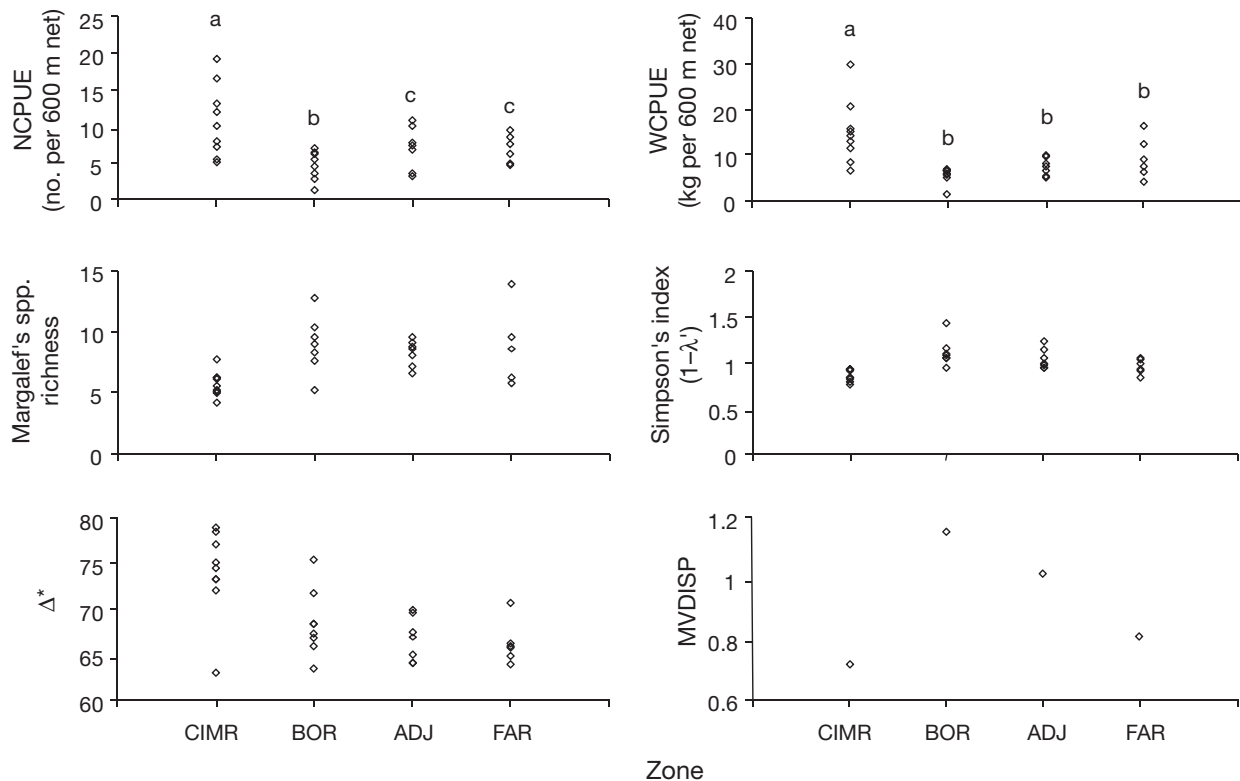

Fig. 4. Annual univariate means of catch per unit effort in numbers (NCPUE) or weight (WCPUE) per 600 m net, Margalef's species richness, Simpson's diversity index, and delta taxonomic distinctness and multivariate dispersal (MVDISP) of the fish community by zone: BOR (border grounds, <0.5 km from CIMR boundary), ADJ (adjacent grounds, 0.5 to 5 km from boundary) and FAR (far grounds, 5 to 30 km from boundary). Letters indicate significant (p = 0.05 level) difference among sites for NCPUE and WCPUE, according to pairwise comparisons (Tukey's HSD test)

8.7) than in the fished zones (BOR mean = 4.8 ± 4.4, ADJ mean = 7.4 ± 8.5, FAR mean = 6.3 ± 4.7) and also that fish abundance in the BOR was significantly lower than in the ADJ and FAR zones, while the latter 2 zones were not significantly different from each other. Fish biomass was also higher in the CIMR (mean ± SD WCPUE = 14.4 ± 13.7) than in the fished zones (BOR mean = 5.7 ± 6.5, ADJ mean = 7.3 ± 7.9, FAR mean = 7.5 ± 7.2), and was lower in the BOR than in the farther
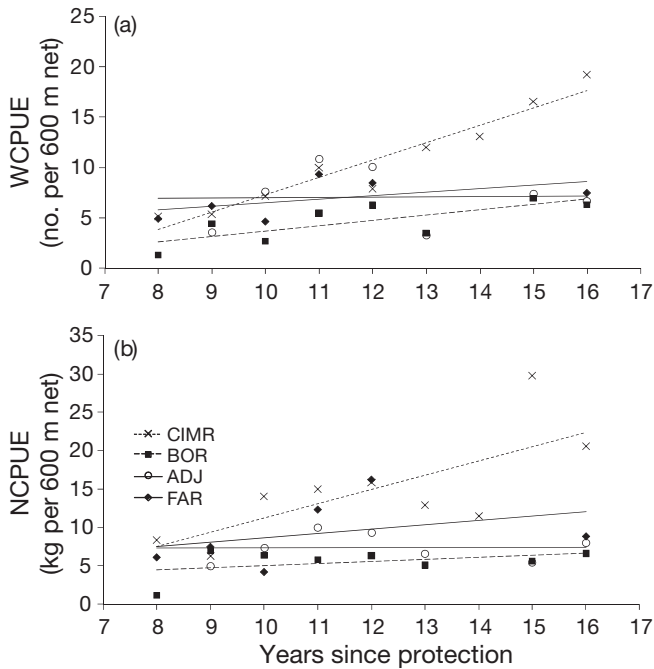

Fig. 5. (a) NCPUE and (b) WCPUE of the fish community as a function of time (years) in the CIMR and nearby fished zones (BOR, ADJ and FAR). Zone definitions and other information as in Fig. 4

Table 3. Results of linear regression analyses of log abundance (NCPUE + 1) and log biomass (WCPUE + 1) as a function of years of protection of the exploited fish community in the CIMR and fished zones (50 to 100 m depth range). BOR: border grounds, ADJ: adjacent grounds, FAR: far grounds (see text for details). Significant p-values are in **bold**

Factor	n	R^2	Slope b	t-statistic	p-value
Abundance					
CIMR	88	0.268	0.068	5.621	**<0.001**
BOR	157	0.085	0.052	3.810	**<0.001**
ADJ	95	0.008	0.013	0.875	0.383
FAR	97	0.033	0.023	1.827	0.071
Biomass					
CIMR	88	0.181	0.061	4.367	**<0.001**
BOR	157	0.037	0.040	2.454	**0.015**
ADJ	95	0.003	0.009	0.584	0.560
FAR	97	0.015	0.020	1.224	0.224

fished zones, although not significantly (Fig. 4). Examined over time, abundance and biomass indices of the fish community in the CIMR increased continuously during the study period and to a lesser extent in the BOR and FAR zones, while there was no change in the ADJ zone (Fig. 5, Table 3). The trend was only significant in the CIMR and BOR zones.

Fish species diversity indices also differed between the CIMR and fished zones. Species richness (Margalef's d) and evenness (Simpson's $1 - \lambda$) had lowest values inside the CIMR and highest at the border zone, with a subsequent weak decline with increasing distance from the CIMR (Fig. 4). In contrast, average taxonomic distinctness measures Δ^* and $\Delta+$ were highest in the CIMR and declined progressively from the BOR, to both the ADJ and FAR zones (Fig. 4).

Frequency distributions of fish relative body size showed that fish were significantly larger inside the CIMR than in the fished zones, while distributions

Table 4. Results of Kolmogorov-Smirnov 2-sample tests of frequency distributions of relative fish body size between zones. Zone abbreviations are defined in Table 3. Significant p-values are in **bold**

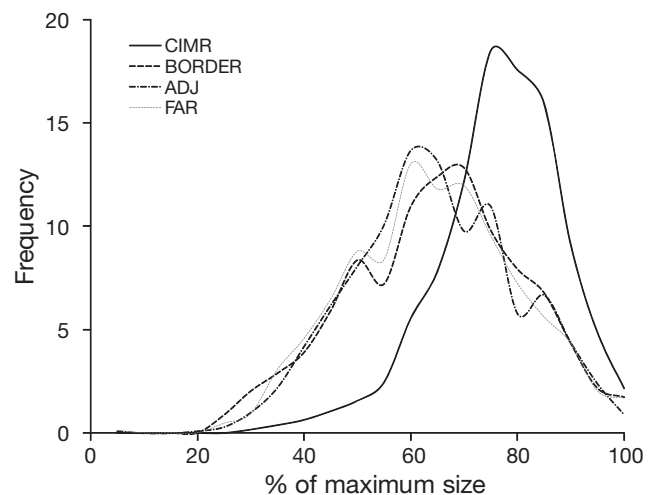| Zone comparison	Z-statistic	p-value
CIMR/BOR	8.567	**<0.001**
CIMR/ADJ	10.745	**<0.001**
CIMR/FAR	12.688	**<0.001**
BOR/ADJ	1.177	0.125
BOR/FAR	1.034	0.236
ADJ/FAR	0.713	0.690

Fig. 6. Percent frequency distributions of relative fish size (expressed as a percentage of the maximum size observed) in the CIMR and nearby fished zones (BOR, ADJ and FAR) (all years combined). Zone definitions and other information as in Fig. 4

were not significantly different among the fished zones (Fig. 6, Table 4). Though fish size distribution at the border did not differ significantly from the other fished zones (Table 4), the distribution did lie between these zones and the CIMR, indicating that the community at the border contained a greater proportion of larger fish than those in the adjacent and far zones (Fig 6).

Initial Kruskal-Wallis analysis revealed that the community in the CIMR had a significantly lower mean trophic level than in the fished zones ($\chi^2 = 28.34$, df = 3, p < 0.001). However, the difference was driven by the presence of large catches of the ray *Raja montagui* within the CIMR, as this species has a relatively low trophic level. When this species was removed from the analyses, there was no difference in mean trophic level between the CIMR and the exploited areas.

Further evidence of differences between the fish communities in the CIMR and fished zones was apparent in the measure of multivariate dispersion (MVDISP), which was lowest inside the CIMR and highest at the border (Fig. 4). MDS plots of yearly averages per zone also showed clear separation of species composition between the CIMR and nearby fished zones (Fig. 7). Two-way ANOSIM tests using zone as one factor and either year, sampling month or distance to the 40 m depth contour as the other, all showed much larger ANOSIM R statistic values for zones than for the other factors (Table 5). Indeed, there was no significant effect of distance from shallow water, with values of the R statistic close to zero. In pairwise zone tests the R statistic was greatest between the CIMR and other zones, and tended to decline in value with increasing distance from the CIMR. Two-way SIMPER analysis with zone and year as factors indicated that the main species accounting for the difference between the CIMR and the BOR, ADJ and FAR zones were *Scorpaena scrofa*, *Raja montagui*, *Zeus faber* and *Lophius piscatorius*.

DISCUSSION

Community change within the CIMR

The recovery time for exploited species in MPAs has important implications for the design of such areas and the management of fisheries (McClanahan et al. 2007). Our results clearly indicate that the exploited fish community in the CIMR changed continuously during the period of 8 to 16 yr after fishing ceased. This temporal change was patent in most community variables studied, with increasing trends of fish abundance and biomass, average body size and, to a lesser extent, changes in species composition. The changes in abundance and species composi-

Table 5. Results of 2-way ANOSIM for fish community differences between year and month groups and distance to 40 m isobath across all zones, and for zone groups across all years, months and distance to 40 m isobath. Zone abbreviations are defined in Table 3

Comparison	Groups	Sample statistic	p-value
Years	Global year	0.084	<0.001
	Global zone	0.079	<0.001
	CIMR/BOR	0.055	0.132
	CIMR/ADJ	0.167	<0.001
	CIMR/FAR	0.228	<0.001
	BOR/ADJ	0.01	0.349
	BOR/FAR	0.085	0.015
	ADJ/FAR	0.066	0.033
Months	Global month	0.048	0.038
	Global zone	0.148	<0.001
	CIMR/BOR	0.27	<0.001
	CIMR/ADJ	0.368	<0.001
	CIMR/FAR	0.264	<0.001
	BOR/ADJ	−0.009	0.606
	BOR/FAR	0.067	<0.001
	ADJ/FAR	0.0	0.471
Distance	Global distance	0.003	0.435
	Global zone	0.085	<0.001
	CIMR/BOR	0.141	<0.001
	CIMR/ADJ	0.155	0.036
	CIMR/FAR	0.321	<0.001
	BOR/ADJ	0.015	0.232
	BOR/FAR	−0.105	0.983
	ADJ/FAR	−0.155	0.998

tion within the CIMR were also evident in the MDS plots, which showed directional change over time and were in stark contrast to our findings outside the CIMR, where there was no evidence of directional change (but see comments on BOR below). Our results are consistent with previous studies of long-term monitoring of MPA fish populations (Russ et al. 2004), space-for-time substitution (Russ et al. 2005, McClanahan et al. 2007) and some meta-analytical work (e.g. Claudet et al. 2008), which indicate that fish density increases with length of time of protection. However, our studies contradict those that show mean responses to protection in MPAs in terms of biomass, mean size or diversity are reached within a few years (Roberts et al. 2001, Halpern & Warner 2002). Our results also show that a stable state had not yet been reached within the CIMR after 16 yr of protection, and that the community properties will most probably continue to change, which again supports studies that suggest recovery can take decades (e.g. Russ et al. 2005, McClanahan et al. 2007).

Abundance and biomass of the exploited fish community grew at an average rate of 14 and 16% per year, respectively, during the study period, without indication of an asymptote. This response has been
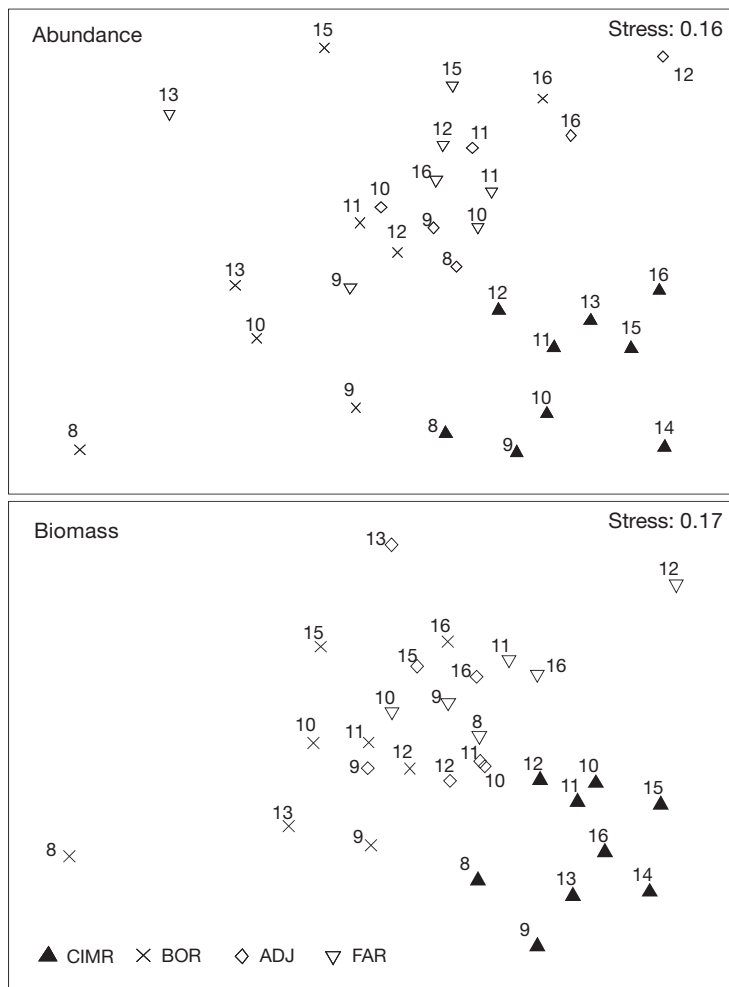
Fig. 7. Multidimensional scaling (MDS) plots of annual average abundance (NCPUE, no. fish per 600 m net) and biomass (WCPUE, kg per 600 m net) of the fish community, with samples represented by zone symbols (CIMR, BOR, ADJ, FAR) and labelled by years since protection. Zone definitions and other information as in Fig. 4

lations. In the CIMR, recreational fishing targets predatory fish (*S. scrofa*, *Dentex dentex*, and *P. phycis* amongst others), which constitute the most valuable bycatch of the spiny lobster trammel net fishery. Recreational fishing, even at relatively low levels, such as allowed in the Columbretes Island Marine Reserve, is known to have a measurable effect on fish populations (e.g. Coleman et al. 2004, Kleczkowski et al. 2008); which strongly supports the need for full fishing closures and good enforcement of MPAs (Guidetti et al. 2008).

Average body size and trophic level of the community also increased during the study period. The progressive growth in the proportion of large fishes in protected populations has been documented in many studies of MPAs in tropical (e.g. Galal et al. 2002, Kaunda-Arara & Rose 2004) and temperate reefs (Harmelin et al. 1995, Tetreault & Ambrose 2007), and is a direct consequence of the reduction of fishing mortality and size-selective fishing (Jennings & Kaiser 1998). Predator removal is one of the most widespread and well-documented direct effects of fishing (Jennings & Kaiser 1998). Thus, in relatively large and well-protected MPAs, such as the CIMR, the observed positive relationship of fish mean trophic level (TL) and time of protection was expected. Most fish species consistently appearing in the CIMR catches are macrocarnivores with trophic levels ranging from 3.30 to 4.55, according to available information (FishBase). The majority of these fishes have gradually increased in abundance over the study period, some remaining low at the beginning and increasing markedly in the later years of the study, among them two with a relatively high TL, *Zeus faber* (TL = 4.40) and *Raja polystigna* (TL = 3.97).

Comparison between the CIMR and fished areas

The comparison of the exploited fish communities in the CIMR with those in fished zones at increasing distances from the CIMR revealed remarkable differences in the patterns of the community variables studied. Firstly, abundance and biomass were highest inside the CIMR and lowest in the border zone, confirming both the predicted recovery of exploited populations inside the CIMR and the local depletion caused

documented in numerous studies in temperate and tropical MPAs (e.g. Sánchez-Lizaso et al. 2000, Russ 2002). Also, as seen in previous studies and model predictions (e.g. Rakitin & Kramer 1996), fish species contributing most to the biomass build up in the CIMR were highly catchable species of restricted to moderate mobility and low resilience, such as the largescale scorpionfish *Scorpaena scrofa*, rays *Raja montagui* and *R. polystigma*, and the great forkbeard *Phycis phycis* (see FishBase). Abundance and biomass in the CIMR increased faster in the latter half of the study period than they did in the earlier half. This may be evidence that recreational fishing, allowed in the CIMR until 2004 (but effectively ceased in 2002 when anchoring was prohibited), had a measurable effect on fish popu-

by commercial effort concentration along the CIMR boundaries. The higher abundance and biomass inside the CIMR in this study was to be expected, as recovery of abundance and biomass of exploited species inside MPAs is an established and widespread phenomenon (Russ 2002, Tetreault & Ambrose 2007) and well studied in Mediterranean MPAs (e.g. García-Charton et al. 2004, Ojeda-Martinez et al. 2007, Harmelin-Vivien et al. 2008). However, although predicted by theory (Walters et al. 2002, Kellner et al. 2007), only a handful of studies have so far documented local depletion of catch rates as a result of effort concentration along MPA boundaries (e.g. MacClanahan & Mangi 2000, Kaunda-Arara & Rose 2004), as observed in this study and the previous study of the lobster fishery around the CIMR (Goñi et al. 2006).

Secondly, the opposite pattern was observed in species richness and diversity and multivariate dispersion (MVDISP), with highest values at the border and lowest inside the CIMR. In the present study lower species richness and evenness were evident inside the CIMR and both were highest in the most heavily fished zone (border), which seems counter intuitive. There is good evidence that fishing leads to depletion of species richness (e.g. Jennings & Kaiser 1998, Hall 1999) and several studies report greater species richness inside MPAs (e.g. Cote et al. 2001, Kaunda-Arara & Rose 2004) or adjacent to MPAs (e.g. Russ & Alcala 1996, McClanahan & Mangi 2000) relative to those in control fished areas. However, there is also evidence to indicate that in some cases fishing may also increase diversity (Bianchi et al. 2000). In our study the lower richness and diversity in the CIMR could be explained by the fact that common bycatch fish species have increased dramatically inside the CIMR, while other species that are occasionally caught in lobster trammel nets have not increased (e.g. *Serranus cabrilla*, *Sparus aurata*), which could lower the value of these indices. In the fished zones, target and main bycatch species have been reduced comparatively more than have species that are occasionally caught, which has the effect of increasing Margalef's richness index (due to lower abundance of fish) and Simpson's evenness index (due to less difference in abundance between species). Nevertheless, recent studies of temperate exploited communities warn that the response of diversity indices to fishing is not straightforward (Rochet & Trenkel 2003, Piet & Jennings 2005). Finally, the pattern of multivariate dispersion (MVDISP) we have observed coincides with studies that report high variability in catches near MPAs (e.g. Abesamis & Russ 2005, Goñi et al. 2006), while greater stability within the CIMR as suggested by MVDISP seems logical as greater year-to-year variation in yields is expected in perturbed systems (Murawski 2000).

A third pattern was observed in taxonomic distinctness (Δ^* and $\Delta+$), which, in contrast to fish species diversity measures, responded positively to protection afforded by the CIMR, with intermediate values at the border and lowest in the adjacent and far zones. We considered that the presence of the ray *Raja montagui* in large numbers inside the CIMR, but rarely outside, could have been the origin of this difference. However, removal of *R. montagui* and subsequently all other rays from the calculation of these indices did not change the trend. Within the Mediterranean Sea Gristina et al. (2006) also found that heavily fished areas showed significantly lower Δ^* and $\Delta+$ values than areas of no or low fishing pressure. On the other hand, Blanchard et al. (2004) found no difference between these indices in strongly versus moderately exploited areas of the Bay of Biscay. Again, conflicting results suggest that further research is needed on the responses of these indices to fishing.

Spillover

The increasing trends in abundance and mean fish size within the CIMR translated into similar upward trends in the yields of the fishery immediately adjacent to the CIMR, providing evidence of the build-up of spillover over time. Among studies that have documented the building up of a spillover effect adjacent to an MPA (e.g. Russ & Alcala 2004, Barrett et al. 2007), ours is the only one that shows this development in conjunction with concentration of fishing effort near an MPA boundary (fishing the line) as documented by Goñi et al. (2006). The combined effect of the 2 processes was local overfishing, with locally depleted, but continuously increasing CPUE at the border (<0.5 km) 8 to 16 yr after CIMR creation without a sign of reaching an asymptote. The upward trend in the border fishery yields was more marked in abundance than biomass and was not apparent in the adjacent (0.5 to 5 km) and far (>5 km) fished zones. While one could argue that CPUE may have increased over time at the border if overall fishing effort was decreasing, we believe that overall fishing effort has remained stable over the study period. This view is supported by the lack of significant temporal trends in abundance and biomass in the adjacent and far fished zones, suggesting that fishing effort in the area has remained stable over the study period. The previous study on lobster spillover from the CIMR showed that about 75% of the commercial fishing effort in the area was deployed within 1 km from the CIMR and also demonstrated local depletion of lobster yields near the boundary relative to farther away (1.5 km) (Goñi et al. 2006).

The fact that the distribution of fish relative body size in the border area lies between that of the CIMR, with the greatest proportion of large individuals, and those of the adjacent and far areas also suggests spillover effects robust to local overfishing. Spillover is also indicated by the 2 measures of taxonomic distinctness that were intermediate between the CIMR and other fished areas, and the fact that the border community followed a nearly significant pattern of seriation, while there was no pattern evident in the adjacent and far zones. Most of the available evidence of spillover comes from spatial comparisons or gradients away from MPAs, with higher catch rates (e.g. Rakitin & Kramer 1996, Russ & Alcala 1996) or catch per unit area (McClanahan & Mangi 2000, Goñi et al. 2006, 2008) of exploited species immediately adjacent to MPA boundaries. In recent years results of studies that examined the development of fish yields or biomass adjacent to MPAs have become available. In an 18 yr study, Russ et al. (2004) found that evidence of spillover close to the Apo reserve was only detectable 8 yr after its establishment. Galal et al. (2002) also reported significant increases in abundance and average size of many targeted reef fishes in 2 of 5 no-take reserves in the Red Sea, with CPUE in the adjacent fished areas increasing by two-thirds over a 5 yr period.

In conclusion, 16 yr after fishing ceased in the Columbretes Islands Marine Reserve, the effects of protection on the exploited fish community were patent and continued to evolve without signs of reaching equilibrium. Fish community trends in abundance, biomass, size structure and species composition were clear, while causes of observed patterns of diversity were more uncertain. The exploited fish community in this MPA and nearby fished zones showed clear differences for most community indicators used. Several indicators show that the fished zone bordering the CIMR is a transitional zone between the CIMR and the fished zones farther away, and that spillover continues to increase in unison with biomass inside the CIMR. In terms of effects of protection on biodiversity, the observed patterns of diversity indices within the CIMR and between zones highlight the need for cautious interpretation. Lower values of traditional species richness (Margalef) and evenness (Simpson) indices within the CIMR would suggest a deleterious effect of protection, while higher taxonomic distinctness measures in the CIMR suggest the opposite. It is becoming clear that species richness and evenness measures alone can be misleading when assessing and evaluating biodiversity change, since, among other limitations, they are heavily dependent on the relative abundances of one or a few dominant species (e.g. Warwick et al. 2002). In making such assessments it is, therefore, helpful to examine as many aspects of biodiversity as

possible to reduce the chance of misinterpretation. The use of population recovery data in MPAs has been hindered by the inability to study well-enforced closed areas over sufficiently long periods in conjunction with suitable control sites (McClanahan et al. 2007). Our study provides a unique case of long-term development in an MPA and comparable fished areas and lends support for the contention that recovery rates are slower and responses stronger than suggested by many short-term studies.

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