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Evaluating the ecological effects of Mediterranean marine protected areas: habitat, scale and the natural variability of ecosystems

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Summary

The capability to detect and predict the responses of marine populations and communities to the establishment of marine protected areas (MPAs) depends on the ability to distinguish between the influences of management and natural variability due to the effects of factors other than protection. Thus, it is important to understand and quantify the magnitude and range of this natural variability at each scale of observation. Here we review the scale of responses of target populations and communities to protection within Mediterranean MPAs, against their 'normal' spatio-temporal heterogeneity, and compare those with documented cases from other temperate and tropical marine ecosystems. Additionally, we approach the problem of the relative importance of habitat structure, considered as a set of biological and physical elements of the seascape hierarchically arranged in space at multiple scales, to drive natural variability. We conclude that much more effort has to be made to characterize heterogeneity in relation to Mediterranean MPAs, and to quantify and explain relationships between target species and their habitats as sources of such variability. These studies should be based on sound sampling designs, which (1) generate long-term data sets, and would ideally (2) be based on a Mediterranean-wide comparison of a number of protected and unprotected localities, (3) be designed from a multi-scaled perspective, and (4) control for factors other than protection, in order to avoid their confounding effects. The need for appropriate spatial and temporal replication, nested designs and power analysis is advocated.

Keywords: marine protected areas, Mediterranean, heterogeneity, scale, habitat structure, sampling designs, target species, fishes

Introduction

Direct and indirect effects of fishing pressure have been reported from both tropical and temperate regions (e.g. Koslow *et al.* 1988; Jennings *et al.* 1995; Rijnsdorp *et al.* 1996; Watson *et al.* 1996; Botsford *et al.* 1997; Myers *et al.* 1997; Goñi 1998). Traditional management measures for sustaining fisheries yields (e.g. catch quotas, mesh size and other gear restrictions) are subject to large errors and biases, attributable to the insufficiency of information, and the complex functioning of marine ecosystems, and so are prone to considerable uncertainty (Ulltang 1998). Marine protected areas (MPAs) have been widely established as an alternative approach to management in the face of this uncertainty (Allison *et al.* 1998; Lauck *et al.* 1998).

The broad effects of the cessation of fishing of target stocks within MPAs are fairly well established both theoretically (see reviews by Plan Development Team 1990; Roberts & Polunin 1991, 1993; Jones *et al.* 1992; Carr & Reed 1993; Dugan & Davis 1993; Agardy 1994; Rowley 1994; Bohnsack 1996; Allison *et al.* 1998) and empirically (e.g. Bell 1983; Russ 1985; Alcala 1988; Buxton & Smale 1989; Alcala & Russ 1990; García Rubies & Zabala 1990; Bennett & Attwood 1991; Polunin & Roberts 1993; Harmelin *et al.* 1995; Roberts 1995; Rakitin & Kramer 1996; Russ & Alcala 1996*a*, *b*; Edgar & Barrett 1997; Piet & Rijnsdorp 1998). However, more complex effects of protection have seldom been verified by field data, notably that MPAs (1) increase local reproductive output and subsequent recruitment in surrounding areas, (2) enhance unprotected populations through outward migration from MPAs, leading to increased catches in adjacent areas, and (3) protect genetic diversity of stocks from fisheries selection (Bohnsack 1996; Allison *et al.* 1998). Furthermore, although the majority of studies have shown some positive effects of protection, other studies have found little, if any, differences between protected and fished areas (e.g. Samoilys 1988; Roberts & Polunin 1992; Dufour *et al.* 1995). Therefore, predictions about the expected effects of particular MPAs cannot be made with certainty.

A major problem arises from the natural heterogeneity of ecosystems (Kolasa & Pickett 1991), and the synergistic effects of the variability of management measures implemented from place to place and through time. Attempts to detect, explain and predict the effects of MPAs should ulti-

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mately be based on statistical tests that distinguish between natural variability and the influence of management (Allison *et al.* 1998). Therefore, studies of the patterns of spatial and temporal variability of targeted and unexploited species, as well as the environmental and biological factors driving this variability are urgently required (García Charton & Pérez Ruzafa 1999). The objectives of the present review were to (1) assess the spatial and temporal scale of responses of fish populations and communities to protection within MPAs, and compare it with what might be described as normal spatio-temporal heterogeneity, and (2) assess the influence of habitat as one obvious source of natural variability. Our ultimate purpose is to address the methodological implications of marine ecosystem heterogeneity for the design of sampling strategies to evaluate the ecological effects of MPAs, and identify the knowledge gaps that must be filled in order to improve the quality of decision-making in research, monitoring, and management of Mediterranean MPAs.

Natural ecological heterogeneity and the effect of MPAs

Measurements of change in abundance, mean size or diversity of target species attributable to protection within MPAs are prone to confounding by natural variability in processes such as natural mortality, migration, egg and larval survivorship, and recruitment. This is particularly true when fishing effects are relatively small. It is often difficult to draw statistically meaningful conclusions from the available data, especially when we consider that estimates of fish density are themselves subject to considerable sampling error (García Charton 1999). What then is the extent of such variability, both spatially and temporally, and how does that compare to the strength of reported 'reserve effects'? This assessment will be made with respect to variations in the abundance of late-juvenile and adult fishes and of early-juvenile fishes.

Adults

The scale of MPA effects in the Mediterranean and elsewhere

The greatest differences between MPAs and ecologically-similar fished areas have tended to be in those species most targeted by fishers, including, in the Mediterranean, *Serranus* spp. and *Diplodus* spp. In studies where such differences have been found, abundances of target fishes as a whole have generally been found to be two to three times greater in MPAs than outside (Bell 1983; Francour 1994; Harmelin *et al.* 1995). Greater abundances of large individuals of target species seem to be particularly good indicators of MPA effects (Table 1). The most prominent example of this comes from Harmelin *et al.* (1995), who found that large target species were almost absent from fished areas close to the Carry-Le-Rouet MPA but were 10 times more abundant within the MPA itself. Similarly, in a study that found no other evidence of the effect of a MPA, Dufour *et al.* (1995) found significantly more large individuals of target fish species in the MPA compared to outside. However, even amongst target groups, the pattern of greater density within MPAs is not universal; for example, Bell (1983) and García Rubies and Zabala (1990) found *Serranus cabrilla* to be most abundant outside of the MPAs which they studied. There is little Mediterranean evidence for effects of MPAs on diversity or species richness. Only two studies have explicitly examined this question, and neither found significant

Table 1 Reported differences in fishes between MPAs and adjacent unprotected areas in the Mediterranean.

Location	*Scale of effect*	*Source*
Banyuls-Cerbère, France	After 6 years' spearfishing ban, reef fish abundance within MPA approximately twice that outside. Amongst target fishes, differences in abundance of 'small' individuals were marginal or non-significant, but for medium and large fishes the differences in abundance were highly significant. No difference in diversity or species richness detected.	Bell (1983)
Banyuls-Cerbère, France	After 18 years of protection, there was no clear difference in abundance of fishes including that of target species. Only difference detected was in abundance of large (30–40 cm) individuals of target species.	Dufour *et al.* (1995)
Scandola, Corsica	Total biomass and density of fishes on rocky substrata within MPA approximately three times that of similar areas outside.	Francour (1994)
Carry-le-Rouet, France	After 10 years of protection, total abundance of demersal species approximately 25% greater within MPA than outside. Target species showed *c.* 2 to 3-fold differences. For the few species for which size data are given (*S. cabrilla* and *C. julis*), mean size in MPA was *c.* 50% greater than outside. The difference in abundance between MPA and outside was *c.* 10-fold for large fishes. Total species richness not significantly higher in MPA than outside, but species richness of target species tended to be approximately twice that outside.	Harmelin *et al.* (1995)

differences between MPAs and unprotected areas (Bell 1983; Harmelin *et al*. 1995).

The pattern and scale of effects of Mediterranean MPAs described above broadly accord with those discerned by the much more numerous studies of reef habitats outside of the Mediterranean. In general, those patterns are for: (1) greater abundances and/or biomasses of fishes within MPAs; (2) larger mean sizes and/or greater abundances of large individuals in MPAs; (3) particularly greater abundance of target species in MPAs; and (4) equivocal evidence for effects of protection on overall species diversity or species richness. Typically, the total density of fishes in areas protected from fishing for four or more years was found to be 2–3 times or more that of adjacent exploited areas (Polunin & Roberts 1993; McClanahan 1994; Roberts 1995; McClanahan & Kaunda-Arara 1996; Rakitin & Kramer 1996; Wantiez *et al*. 1997). In general, the reported differences in biomass are large or greater than those in numerical abundance because MPAs tend to have both greater abundances and greater average sizes of fishes (e.g. Polunin & Roberts 1993; Russ & Alcala 1996*a*, *b*). In one of the few long-term studies to date, Russ and Alcala (1996*a*) found that the increase in biomass over time within two MPAs in the Philippines was more curvilinear than the increase in fish abundance; there was a slow increase in fish biomass in the first 3–5 years of protection, followed by a more rapid increase in the next four years. The initially slow increase in biomass was related to (1) delayed recruitment effects meaning that fish abundance took time to increase, and (2) in the first few years of protection, fish stocks were dominated by very young fish that did not accumulate as much biomass as fishes aged 2–4 years (Russ & Alcala 1996*a*). Relatively few studies of MPAs present results on diversity and those results that exist have been somewhat equivocal. Wantiez *et al*. (1997) in a study of protected and fished areas in New Caledonia found a 64% increase in species richness within MPAs after five years of protection but no similar increase in reference areas. In contrast, Roberts and Polunin (1992) found that Red Sea MPAs protected from fishing for 15 years did not have greater species richness than fished sites. Presumably, local factors including the intensity of fishing outside of the MPAs and effectiveness of protection, are important factors. It is also important to note that not all studies show any clear ‘reserve effect’; for example, Samoilys (1998) could not detect a difference between fished and protected areas on the east coast of Kenya after 20 years of apparently successful protection from fishing. The lack of difference was attributed to other factors such as heavy siltation, any ‘reserve effect’ being

Table 2 Large-scale spatial variation in abundance (/100 m^2) of common target species on rocky slopes in MPAs and unprotected localities in the western Mediterranean. Figures in parentheses refer to abundances of other *Serranus* species cited in bibliographic references.

Location (study) (range of depth)	*Abundance of target species*				
	Serranus cabrilla (other Serranus)	*Coris julis*	*Diplodus spp.*	*All fishes*	*Species richness*
Sites within MPAs					
Banyuls-Cerbère, France (Bell 1983) (7–20 m)	1.1–2.1	13.7–31.7	6.3–6.8	102.7–115.9	31.3
Medes Islands, Spain (García Rubies & Zabala 1990) (6–9 m)	3.8	20.5	57.0	–	–
Carry-le-Rouet, France (Harmelin *et al*. 1995) (9–14 m)	3.7	41.4	28.0	426.6	50
Port Cros, France (Harmelin 1987) (10–15 m)	–	20.4–22.7	13.2–30.0	211.4–221.2	47
Tremiti Islands, Adriatic Sea (Fasola *et al*. 1997) (14–42 m)	0.8 (0.5)	15.7	0.7	92	39
Cape of Palos, Spain (García Charton & Pérez Ruzafa 1998) (3–15 m)	0.1 (1.6)	9.4	4.8	231.2	40
Non-MPAs					
Banyuls-Cerbère, France (Bell 1983) (7–20 m)	1.9–3.2	13.1–17.1	2.0–3.4	48.0–58.1	27
Falaguer, Spain (García Rubies & Zabala 1990) (6–9 m)	7.0	15.5	7.5	–	–
Cape Bear, France (Harmelin *et al*. 1995) (9–14 m)	1.4	26.0	9.2	230.9	43

Table 3 Mean species richness, biomass (g 250 m^{-2}), and numerical abundance (individuals 250 m^{-2}) of each species and of all species combined in fish assemblages (target species signalled by *) censused at seven Spanish localities included in a hierarchical sampling design involving four MPAs (CP = Cabo de Palos, CG = Cabo de Gata, CB = Cabrera, CL = Columbretes) and three unprotected areas (IG = Isla Grosa, AG = Aguilas, ML = Mallorca). Results from the spatial nested analysis of variance are also shown, indicating the spatial scales at which significant variation exists (LOC = localities, SECT = sectors within localities, ZONE = zones within sectors) (*** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$, ns = not significant) (J.A. García Charton, P. Sánchez Jerez, O. Reñones, J.T. Bayle Sempere & D. Moreno, unpublished data 1996).

	CP	*CG*	*CB*	*CL*	*IG*	*AG*	*ML*	*LOC*	*SECT*	*ZONE*
All species										
Mean species richness	14.2	15.7	19.3	18.1	11.9	17.3	15.6	**	ns	***
Mean abundance	951.3	781.5	466.9	939.2	488.7	921.2	445.0	*	*	**
Mean biomass	109 700	71 430	23 960	95 550	10 210	28 290	7224	**	ns	*
Individual species										
* *Engraulis encrasicolus*	–	2.1	–	–	37.0	23.8	–	ns	ns	**
* *Muraena helena*	0.8	0.4	0.5	0.3	0.04	0.2	0.4	ns	*	*
* *Conger conger*	–	0.04	–	–	–	–	–	ns	ns	ns
Phycis phycis	0.04	0.04	–	–	–	0.04	–	ns	ns	ns
Anthias anthias	65.1	–	4.4	–	–	18.7	–	ns	***	***
* *Epinephelus costae*	0.1	2.4	0.2	–	0.1	0.1	–	***	ns	*
* *Epinephelus marginatus*	0.2	1.6	2.3	2.1	0.1	0.6	0.1	***	*	ns
* *Epinephelus caninus*	–	0.2	0.1	–	–	0.1	0.04	ns	ns	***
* *Mycteroperca rubra*	–	–	–	0.4	–	0.04	–	ns	ns	ns
* *Serranus atricauda*	0.04	0.3	–	–	–	–	–	***	ns	ns
* *Serranus cabrilla*	2.3	3.8	2.4	1.2	1.5	1.3	1.3	ns	*	ns
* *Serranus scriba*	1.2	6.0	3.0	3.9	2.3	3.9	3.5	**	**	ns
Apogon imberbis	8.2	18.5	7.2	1.7	4.1	68.7	3.3	**	ns	**
* *Seriola dumerilii*	–	0.04	0.04	5.9	–	2.9	–	ns	ns	***
* *Trachurus mediterraneus*	0.3	–	–	–	–	–	–	ns	ns	ns
* *Coryphaena hippurus*	0.04	0.04	–	–	–	–	–	ns	ns	ns
Parapristipoma octolineatum	–	3.5	–	–	–	0.3	–	ns	ns	***
Pomadasys incisus	0.04	–	–	–	–	–	–	ns	ns	ns
* *Sciaena umbra*	0.9	1.7	0.4	18.6	0.04	0.9	0.04	***	ns	***
* *Mullus surmuletus*	0.5	8.9	2.1	0.9	1.3	4.3	0.8	ns	***	ns
* *Boops boops*	13.1	132.0	25.8	275.2	20.0	86.4	49.7	ns	***	ns
* *Dentex dentex*	2.9	–	0.1	21.9	–	0.1	0.4	***	ns	***
* *Diplodus annularis*	1.4	0.2	7.8	–	1.4	5.0	5.2	**	**	**
* *Diplodus cervinus*	0.3	0.3	–	–	–	0.1	–	*	ns	***
* *Diplodus puntazzo*	3.5	0.6	0.9	0.04	1.4	3.2	0.4	ns	**	ns
* *Diplodus sargus*	9.5	2.0	3.4	0.6	2.6	14.0	2.8	**	ns	***
* *Diplodus vulgaris*	25.0	43.7	28.1	26.9	14.3	25.4	12.1	ns	ns	***
* *Oblada melanura*	33.3	37.0	6.7	20.6	4.6	75.8	6.5	ns	**	**
* *Pagellus acarne*	–	–	–	–	–	1.7	–	ns	ns	ns
* *Pagrus pagrus*	0.04	0.04	–	0.1	0.04	1.0	–	ns	ns	***
* *Sarpa salpa*	37.7	9.7	22.0	13.7	4.4	35.5	19.8	ns	***	ns
* *Sparus aurata*	0.04	–	0.04	1.0	–	–	–	*	*	***
* *Spondyliosoma cantharus*	0.1	–	1.4	6.5	–	–	1.0	***	ns	ns
* *Spicara flexuosa*	–	–	5.4	0.3	6.3	53.0	2.9	ns	ns	ns
* *Spicara smaris*	–	–	–	1.0	–	1.5	–	ns	ns	ns
Chromis chromis	527.7	347.9	274.0	465.5	308.2	411.1	292.8	ns	**	ns
Coris julis	32.7	70.7	23.5	17.0	25.9	39.2	20.0	***	ns	**
* *Labrus merula*	0.04	0.04	0.6	0.8	0.1	–	0.04	*	**	ns
* *Labrus viridis*	–	–	0.3	0.2	0.04	–	0.04	**	ns	ns
Symphodus cinereus	–	0.1	–	–	–	–	–	*	ns	ns
Symphodus doderleinii	0.04	0.4	0.1	0.3	–	0.5	0.04	***	ns	ns
Symphodus mediterraneus	0.5	0.7	2.1	2.9	0.1	1.1	2.7	***	ns	***
Symphodus melanocercus	–	0.04	0.7	0.4	0.2	0.4	1.1	***	ns	ns
Symphodus ocellatus	2.6	9.1	7.3	11.5	4.7	7.0	3.3	ns	***	ns
Symphodus roissali	0.4	0.8	0.9	0.9	0.5	0.6	0.7	ns	**	ns
Symphodus rostratus	0.1	1.6	0.6	0.1	0.3	1.1	1.4	***	ns	ns
* *Symphodus tinca*	2.6	10.6	4.3	4.4	5.8	9.0	5.3	*	*	*

Table 3 – continued

	CP	*CG*	*CB*	*CL*	*IG*	*AG*	*ML*	*LOC*	*SECT*	*ZONE*
Thalassoma pavo	99.1	32.2	10.9	16.1	40.6	22.0	6.6	**	*	*
* *Sarda sarda*	–	–	–	1.6	–	–	–	ns	ns	ns
* *Sphyraena sphyraena*	40.3	31.9	15.7	11.9	0.3	–	0.3	*	ns	***
* *Mugilidae spp.*	0.9	0.4	1.4	2.6	0.3	0.7	0.4	ns	ns	ns
* *Scorpaena porcus*	0.7	–	–	–	–	–	–	ns	ns	ns
* *Scorpaena notata*	–	0.04	0.04	–	–	–	–	ns	ns	ns
* *Scorpaena scrofa*	–	–	–	–	–	0.04	–	ns	ns	ns
Balistes carolinensis	–	–	–	–	–	0.1	–	ns	ns	***
Atherina hepsetus	37.0	–	–	–	–	–	–	ns	ns	***

confounded by differences in environment amongst the areas compared (Samoilys 1988).

Spatio-temporal variability of Mediterranean fish populations

At the scale of typical censuses (i.e. tens of metres, over periods of from minutes to hours), considerable spatio-temporal heterogeneity in fish populations data is evident. With sufficient sampling, real differences in fish density amongst areas or time periods should be detectable, but, in the absence of controlled time-series data, the question as to whether any differences are a consequence of protection or are merely coincidental, will always remain. As an example of how this can be a problem, Bell (1983) found fish abundance within the Banyuls-Cerbère MPA to be approximately twice that of reference areas outside the MPA, but 12 years later, no such pattern was found (Dufour *et al*. 1995). Without knowing the normal scale of temporal variability, we cannot say whether (1) the initial difference was large in comparison to normal spatial heterogeneity, in which case we might conclude that protection had been effective at the time of the initial surveys but had become less so since, or (2), alternatively, natural heterogeneity was large in comparison to the initial difference between MPA and unprotected areas, in which case studies at greater temporal and possible spatial scales would be necessary to determine confidently whether the MPA actually had been effective in enhancing fish abundance. When it comes to drawing conclusions about more complex effects of protection, such as secondary effects on non-target species, the problem is even greater since even less is known about the likely scale of the effects of protection in MPAs on these groups. Sasal *et al*. (1996) reported greater mean size of a non-target species, *Gobius buchichii*, within the Banyuls-Cerbère reserve and took this to be evidence of an indirect effect of protection. Such a conclusion would be greatly strengthened if the reported difference could be shown to be large in comparison with the normal heterogeneity that is unrelated to protection.

At very large spatial scales (i.e. hundreds to thousands of km), there are substantial differences in abundances of those ‘target species’ that previous studies have indicated are probably the best indicators of the effects of MPA protection. For example, amongst six studies of Mediterranean MPAs, density of all fish or of particular species (such as *Coris julis*) varied amongst areas by a factor of four or more, and for individual target groups, the scale of variation could be considerably larger (40 to 80-fold for *S. cabrilla* and *Diplodus* spp.) (Table 2). At such spatial scales, natural variability is almost certainly greater than any differences between MPAs and unprotected areas and so comparisons at this scale are not likely to be useful. It is therefore worth considering what degree of spatio-temporal heterogeneity might be expected at scales relevant to those of the effects of MPAs, in other words spatially at medium to large scales (i.e. hundreds of metres to several kilometres) and temporally at the seasonal and inter-annual levels. Unfortunately, there are very few studies from the Mediterranean that contain comparative data from similar sites at the same level of protection (where difference can be attributed to real spatial heterogeneity) and even less of the kind of information that would help to reveal the normal level of temporal variability.

In the only multi-scaled study of Mediterranean rocky reef fishes of which we are aware (García Charton 1999), the abundance of 15 out of 40 target species differed significantly in spatially nested analysis of variance (ANOVA) amongst seven localities situated tens to hundreds of kilometres apart (Table 3). The hierarchical sampling design allowed the components of variation to be partitioned amongst spatial scales, and the scales that contributed most to the total variation could be identified. For instance, variation in densities of serranid species amongst localities ranged from 3-fold for *S. cabrilla* to approximately 25-fold for *Epinephelus costae* and *E. marginatus*. Several species, for example *Mycteroperca rubra*, *S. atricauda*, and *Parapristipoma octolineatum*, were observed in only a few localities. Additionally, the total number of species and individuals, and total biomass, also showed spatial heterogeneity at a similar scale. Interestingly, one of the unprotected areas (Aguilas, Murcia, SE Spain) had values of species richness and abundance that were comparable to those observed in the four MPAs (Cabo de Gata, Cabo de Palos, Cabrera and Columbretes). Spatial heterogeneity was evident also at other scales, namely amongst sectors placed thousands of metres apart within each locality, and amongst zones separated by hundreds of metres within each sector (Table 3). Thus, abundance of 13 out of 40 target species differed significantly amongst sectors, and abundance of 17 target species differed significantly amongst zones. For 14 of the target species, there were differences at more than one spatial scale (Table 3), so that in all it was possible to detect a significant spatial patterning at some scale for 28 target species. The portion of total variance that was not explained by spatial (nested) factors was attributable in part to spatial variation occurring at smaller scales, namely amongst replicate transects separated by tens of metres.

Other evidence of 'normal' spatio-temporal variability amongst relatively close locations (separated by <10 km) comes from two studies by Harmelin (1987, 1990) in which fish communities at different sites within the Port-Cros MPA were compared at different times of the year. Between the two sites surveyed, the abundances of 10 out of the 16 most common species differed by a factor of two or more, and for 5 of the 16, by a factor of three or more (Harmelin 1987). Similarly, spatial heterogeneity in abundance of fishery-target species (*S. cabrilla*, *Diplodus vulgaris* and *C. julis*) amongst the four sites surveyed was between 2.5 and 3.4 (Harmelin 1990). For some species, however, the differences in abundance amongst sites were much greater, for example 9-fold for *Chromis chromis* (Harmelin 1990) and 50-fold for *Sarpa salpa* (Harmelin 1987), although spatial heterogeneity was much lower when fishes were grouped into functional categories. Differences between sites were greatest for schooling fishes (categories 1 and 2 of Harmelin 1987) for which differences were 2 to 3-fold, and least for fishery-target groups (categories 3 and 5, which included *Diplodus* spp., labrids and serranids); the differences in abundance between locations for those categories were approximately 30–40% (Harmelin 1987).

The few data on temporal patterns make it even more difficult to draw firm conclusions about what the normal scale of seasonal and annual variation might be. However, at least for some groups, seasonal variation can be considerable, for example 4-fold for open-water schooling species such as *Boops boops* and *Oblada melanura* (Harmelin 1987) and up to 25-fold for *C. chromis* (Harmelin 1990); some species present in samples at certain times of the year will be absent at others (Harmelin 1990). For some species, including such target species as *S. cabrilla* and *Diplodus* spp., seasonal changes in abundance appear to be much less. For example, between three seasons at each of two sites, abundance generally differed by around 10–50% for these groups (Harmelin 1987). The pattern of seasonal variability did not appear to be the same at all sites; for example, in November compared to March, category 1 fishes (schooling, erratic species living in the water column, such as *B. boops* and *Spicara* spp.) were 50% more abundant at La Galère but only a quarter as abundant at Malalongue (Harmelin 1987). In fact, amongst the common species for which data were presented, few had a consistent pattern of seasonal difference (Harmelin 1990). At the only location for which interannual data were available, very few differences were observed between March 1985 and March 1986 (Harmelin 1987). Mean total abundance (all fishes) varied between 720 and 730 per survey for these two periods, and for only one out of six species for which data were presented (*C. julis*) was there a significant difference between years, and even then the difference was only 30% (Harmelin 1987).

Non-Mediterranean studies

There is little evidence of what might be considered normal spatio-temporal heterogeneity from studies outside of the Mediterranean. What evidence there is suggests that substantial spatial heterogeneity is common at the species level; for example, Letourneur (1996*a*) found significant differences in abundance for 11 of 22 species amongst three fringing-reef sites separated by approximately 35 km at La Réunion, Indian Ocean. However, as appears to be the case for studies in the Mediterranean, amongst-location patterns were more consistent when species were grouped into higher taxonomic or functional categories (e.g. Jennings & Polunin 1997). Studies that have monitored fish communities over a number of years have indicated variations in total fish abundance between years of 75–90% over seven years (Galzin 1987*b*) and 16–37% at sites which were revisited after 13 years (DeMartini *et al.* 1996). For individual genera, between-survey differences can be much greater, for example 50-fold for *Priacanthus* and 12-fold for *Chromis* (DeMartini *et al.* 1996). Seasonal patterns of fish abundance deduced from reef studies outside of the Mediterranean also show complex variation, with different patterns for different reef zones and species (Galzin 1987*b*). Considerable variation in abundance between seasons appears to be normal for many species; for example Letourneur (1996*b*), in a study of temporal variation in fish communities on fringing reefs at La Réunion, found significant differences between survey periods (summer and winter of 1989 and 1990) for 14 out of 22 species for which data were given, and for only six of those species was there a consistent seasonal pattern. In all cases, abundance in summer was greater than in winter (Letourneur 1996*b*). Some species undergo regular seasonal migrations, and for these the differences in local density between seasons can be naturally large, for example 10-fold between seasons in the abundance of snappers (Diaz-Ruiz *et al.* 1996). Other temporal patterns such as lunar periodicity may also be important for some species. For example, Galzin (1987*b*) found that 30% of the variability amongst fish censuses at different times could be explained by lunar periodicity, and similarly, Letourneur (1996*b*) noted increased species richness and abundance during full moon periods.

While the spatial and temporal variability of fish abundance data is marked at the species level, fishing and protection effects have tended to be clearer at aggregate levels such as those of families and trophic groups (e.g. Polunin & Roberts 1993; DeMartini *et al.* 1996; Jennings & Polunin 1997). Yet the extent to which differences between species and group levels result from the sampling methodology, or are a measure of (for example) ecological equivalence of species, is not known.

Recruitment

Temporal and spatial variations in abundance of large juvenile and adult animals may be contributed to by migration (e.g. Bayle Sempere *et al.* 1994) and/or by fluctuations in recruitment. The latter may occur through changes in egg output (Bagenal 1973), in abundance of larvae (Doherty 1991), in site-selection by settling larvae (Fowler *et al.* 1992), in survivorship of juveniles once settled (Shulman & Ogden 1987), or combinations of these (Jones 1991).

In the Mediterranean, large differences in recruitment have been found amongst years in the sea urchin *Paracentrotus lividus* (López *et al.* 1998), and in three *Diplodus* spp. also amongst sites separated by hundreds of kilometres in the north-western Mediterranean (Macpherson *et al.* 1997). Interannual variability in the sea urchin was attributed substantially to differences amongst years in food availability to the larvae (López *et al.* 1998). The abundance of newly-settled fish varies seasonally, with strong seasonality in some species (e.g. the wrasses *Symphodus* spp.), while in other species (e.g. *D. vulgaris*) settlers may be abundant at more than one time and/or over a more extended period (García Rubies & Macpherson 1995). Although most recruitment occurs in the summer (July–September), recruitment of *Diplodus* spp. on the north-eastern coast of Spain appears to be temporally segregated amongst species (García Rubies & Macpherson 1995). As they increase in size, *Diplodus* spp. move into deeper water and, amongst sparids as a whole, shoal size either increases (*O. melanura* and *S. salpa*) or decreases (*Diplodus* spp.) (Harmelin-Vivien *et al.* 1995). The study of Macpherson *et al.* (1997) indicated that variability in year-class strength is greatly reduced in a density-dependent fashion during the early juvenile stage of *D. puntazzo* and *D. sargus*, but not in *D. vulgaris*. Most post-settlement mortality in the sea urchin *P. lividus* (López *et al.* 1998) and in *Diplodus* occurred in the first two months, and the indication is that year-class strength was probably set largely by processes prior to settlement, and its variability was much reduced in the few weeks after it (Macpherson *et al.* 1997). Recently-settled individuals of *Diplodus* spp. are fed upon by various invertebrates and fishes, but the fishes involved were mostly small and there was no evidence of any difference between MPAs and unprotected areas, although predation is expected to be more intense in the former (Macpherson *et al.* 1997). Growth rate of settled *Diplodus* spp. (5–80 mm total length) varied amongst sites separated by hundreds of kilometres and amongst species, but not between two years (Planes *et al.* 1999).

Recruitment fluctuations have been described by many studies outside of the Mediterranean (e.g. Doherty & Williams 1988; Booth & Brosnan 1995). The phenomenon of strong and weak recruitment year classes has long been recognized (e.g. Heath 1992). In temperate waters, strong year classes can contribute greatly to stock density (e.g. Bailey 1981), and, although as yet poorly documented for fishery species (e.g. DeMartini 1995), the same effect of temporal change in recruitment exists even in a large tropical fish which lives for up to 15 years (Russ *et al.* 1996). Such variations in adult biomass are likely to be contributed to by variable egg production, egg and larval survivorship, larval site-selection, and juvenile survivorship. It is generally accepted in marine population ecology that relationships between spawner abundance and recruitment intensity are poorly developed; recruitment is much more variable than is egg output and recruitment is predictable in many cases from larval supply to the settlement habitat and not from the abundance of adults (e.g. Meekan *et al.* 1993; Robertson *et al.* 1993; Hughes *et al.* 1999).

Outside of the Mediterranean, there is some evidence that the variability of fish larvae from the plankton may be greatest at very small (e.g. < 3 km) and very large (e.g. > 250 km) spatial scales, while at intermediate scales (e.g. 10–15 km), it may be much lower (e.g. Doherty & Williams 1988; Doherty 1991; Lincoln Smith *et al.* 1991; Hughes *et al.* 1999). At intermediate scales, recruitment may be relatively deterministic, affected for example by food availability for the larvae (e.g. Thresher *et al.* 1989) or advection (Williams *et al.* 1984; Thorrold *et al.* 1994), and spatial differences in processes such as these may help drive the large-scale differences (hundreds of kilometres) in larval supply. Relevant oceanographic processes such as advection are subject to episodic and local reversals (e.g. Sabatés & Maso 1992; Álvarez *et al.* 1996) that may have pronounced spatial and temporal effects on recruitment when coinciding with recruitment events.

At smaller spatial scales (e.g. < 3 km), habitat characteristics may become important (e.g. Victor 1986; Levin 1991), so that management practices and other human impacts may indirectly affect abundance through impacts on recruitment. The small size of samples used to quantify recruitment may also be a factor in variability where it occurs at spatial scales that are large relative to sample areas. It follows that management of a particular MPA could vary according to whether samples were in areas of low or high recruitment, and, further, that detecting impacts of management may rely crucially on the sampling design used for monitoring.

Processes acting subsequent to settlement, such as predation (Carr & Hixon 1995), may also be important in determining recruitment; in some cases, these processes may contribute to regulation and lead to reduced interannual variability in abundance (e.g. van der Veer & Bergman 1987). There is considerable scope for feedback effects of area protection on the outcomes of management (e.g. McClanahan 1994), even if to date, for example, Mediterranean data on sparids have not shown effects of MPAs on recruitment (Macpherson *et al.* 1997).

Concluding remarks

Heterogeneity at spatial and temporal scales similar to those from which evidence of MPA effects has been derived is probably common. There are surprisingly few data on this heterogeneity in relation to Mediterranean MPAs. There is need for (1) long-term data sets within reserves and unprotected areas within the entire Mediterranean, and (2) realistic assessment of what the relevant scales of natural variability are. If effects of MPAs are to be correctly identified and their nature reliably predicted, sampling and monitoring designs involving considerable replication in space and time are essential.

Because of large-scale variation at the species level, conclusions about effects of MPAs based on abundance at the level of individual species should only be arrived at with caution, and in assessment of MPA effects, it is probably wise to focus on larger individuals of species that are susceptible to fishing. In the design of realistic monitoring programmes, it makes sense to aggregate species-level data, into families or trophic groups for example, but the implications of this aggregation for what is happening at species level are unclear. Seasonal and lunar fluctuations in abundance and recruitment of benthic animals such as fish are probably important for at least some species. Comparisons aimed at quantifying MPA effects specifically need therefore to be made amongst sites as spatially and temporally close together as possible, and ideally, multiple MPAs should be compared with multiple unprotected areas. Both types of area should ideally be sampled at a range of spatial and temporal scales, in order to take account of the multiscaled natural variability of the descriptors chosen as indicators of the effects of protection from fisheries.

Because there are always environmental, including habitat, differences amongst sites and time periods being compared, it is difficult to distinguish stochastic spatio-temporal heterogeneity from deterministic effects, whether of environment or management. It appears, however, that protection in MPAs may have feedback effects on processes such as recruitment, for example where recruitment is influenced by habitat, and habitat is influenced directly and/or indirectly by exploitation.

Habitat and scale: pattern and processes in spatially explicit terms

If we consider habitat structure from a functional perspective, in other words by considering habitat to be any physical or biological environmental attribute that offers some resource such as food or shelter to the organisms of interest at a given scale (McCoy & Bell 1991; Jones & Andrew 1992), then it is pertinent to ask what features of this habitat are important to those organisms, and what are the responses of those organisms to spatio-temporal heterogeneity of a feature of this habitat. A realistic assessment of the influence of habitat variability should be an important component of any attempt to distinguish MPA effects from other sources of heterogeneity. In the following sections we review documented responses of targeted species to habitat variability, and, more briefly, consider how protection activities can themselves alter habitat.

Habitat and Mediterranean target species

When viewed at certain spatial scales (10^3–10^4 m), several bottom types can be distinguished in the Mediterranean littoral, namely soft substrata (mud, silty sand, sand, gravels and pebbles), whether colonized or not by the seagrasses *Posidonia oceanica* or *Cymodocea nodosa*, and rocky reefs. By reducing the scale of observation additional details could be distinguished within each bottom type. Mediterranean rocky bottoms are generally formed by boulders of several sizes (from small stones to huge blocks) resulting from coastal erosion, flagstones, plates or large areas of bedrock with varying degrees of architectural complexity. Successive reductions of the scale of observation would help to reveal new details of complexity as a result of the fractal geometry of rocky landscapes (Bradbury & Reichelt 1983; Bradbury *et al*. 1984). Habitat complexity can thus be measured at each scale using different variables (e.g. number of boulders classified by size, rugosity, and so on). The complexity of coastal rocky bottoms is enhanced by habitat 'formers', defined as 'those species that characterize a habitat' (Jones & Andrew 1992) which provide additional resources such as physical refuge and food items to target species (Sebens 1991; García Charton *et al*. 1999). These structural species are algae (Gee & Warwick 1994; Chemello & Russo 1997) and animal species, such as sponges (Koukouras *et al*. 1996), cnidarians (e.g the zooxanthellate scleractinian *Cladocora caespitosa* [Arvanitidis & Koukouras 1994; Peirano *et al*. 1997; Koukouras *et al*. in press]) and the gorgonians *Paramuricaea clavata*, *Eunicella cavolinii* and *E. singularis* (Russo 1985; Burlando *et al*. 1991; Mistri 1994; Skoufas *et al*. 1996), and the midlittoral vermetid platforms formed by the gastropod *Dendropoma petraeum* and the red alga *Spongiolithon mediterraneum* (Safriel & Ben-Eliahu 1991; Pandolfo *et al*. 1996).

Despite the fact that soft bottoms harbour low structural complexity, they can contain a wide spectrum of roughness, at scales ranging from 10^{-3} to 10^3 m (Akal 1984). A kind of structural complexity on soft bottoms is caused by benthic organisms as a result of their burrowing activities or merely by their conspicuous presence (Sebens 1991). Some species can even form distinct, particularly complex substrata, such as those formed by the bivalve *Ervilia castanea* in coarse sand, which are colonized by a wide array of organisms (Moreno 1998), and the corallinacean (*Mesophyllum lichenoides*) bioconcretions that support a number of associated molluscan species that varies with changes in their shape (Hergueta & Salas 1987). Particularly important is the Mediterranean *maërl*, formed by a substantial number of species (Augier & Boudouresque 1978; Ballesteros 1988; Di Geronimo & Giaccone 1994). The most important biogenic habitats for targeted species on soft bottoms are the seagrass meadows of *P. oceanica*. First attempts to study their spatial structure were done by merely distinguishing between small (microstructural) (e.g. measurement of shoot size, shoot density, average length or elevation beneath the sediment) and medium-to-large (macrostructural) scales (e.g. coverage [Giraud 1977; Panayotidis *et al*. 1980, 1981; Meinesz *et al*. 1981; Romero 1985]). The spatial pattern of *P. oceanica* meadows has often been described by characterizing formations in different ways such as various types of lower limits (Colantoni *et al*. 1982), 'hills' (Boudouresque *et al*. 1985*a*), 'barrier-reefs' (Boudouresque *et al*. 1985*b*), 'cordons' (Vetere & Pessani 1989), and 'atolls' (Calvo & Fradà-Orestano 1984).

Nevertheless, these 'static' spatial structures seem to be nothing but particular solutions of the spatial pattern resulting from interactions between the dynamic processes of seagrass populations (e.g. recruitment, clonal growth and mortality) and a variety of local environmental factors that control its abundance. Thus, more fruitful images could be obtained by studying the habitat structure determined by seagrasses under a hierarchical, multiscaled approach (Duarte & Sand-Jensen 1990; Robbins & Bell 1994; Bell *et al.* 1995; Vidondo *et al.* 1997), distinguishing between individual shoots (10^{-2} m), clumps (10^{-1}–10^{0} m), beds (10^{1}–10^{2} m) and meadows (10^{3}–10^{4} m), and investigating the different processes affecting seagrass dynamics over this continuum of scales.

Responses of fishes to variations of habitat structure in the Mediterranean

Although several studies of Mediterranean fish assemblages have sampled within clearly defined habitat types, namely *P. oceanica* meadows (e.g. Bell & Harmelin-Vivien 1982; Harmelin-Vivien 1982; García Charton *et al.* 1993; Bussotti & Guidetti 1996; Francour 1997) and rocky bottoms (e.g. Bell 1983; Harmelin 1987, 1990; Jouvenel 1992, 1997; García Rubies 1997; Spyker & van der Berghe 1995; Reñones *et al.* 1997), there is nonetheless a general lack of data specifically quantifying the relationship between Mediterranean fishes and spatio-temporal variability in habitat structure. The few studies to specifically address this problem have generally been carried out at very small spatial scales on non-target species (Kotrschal 1988; Macpherson 1994). The influence of depth on local Mediterranean rocky-reef fish assemblages was first described by Bell (1983), and subsequently studied by Jouvenel (1997) and García Charton and Pérez Ruzafa (1998), while Harmelin (1990) compared a deep 'coralligenous' fish assemblage with the results of his previous studies on shallower sites in the same area. These studies indicate that a substantial part of the differences found in local densities is due to the preference of non-perturbed populations for shallow, more productive bottoms, combined with the effects of fishing pressure compelling vulnerable species to move into deeper water; however, much more work is necessary if depth distributions are to be understood.

Regarding rocky substrata, Harmelin (1987) proposed that local fish species richness increases with increase in habitat complexity after comparing two sites of low and high relief in Port-Cros National Park. García Rubies (1997) found significant differences in species richness and abundance of species classified by spatial categories amongst sites that differed simultaneously in the degree of protection from fishing and in substratum complexity. For their part, García Charton and Pérez Ruzafa (1998) estimated that 40% of the variability in species richness (Fig. 1), and 70% of total fish abundance, could be accounted for by amongst-location variations in habitat complexity, as measured by the number of rocky boulders of several sizes inside 250 m^2 transects. However, habitat heterogeneity, estimated as the percentage cover of different substratum types (rock, sand and *P. oceanica*), did not appear to influence either abundance or richness of fish assemblages, possibly, because fish assemblages were influenced by habitat variability at scales both larger and smaller than those used in the study (García Charton & Pérez Ruzafa 1998). When the same problem was studied at a smaller spatial scale (50 m^2 quadrats) in the same area (Cabo de Palos, Murcia, SE Spain), García Charton (1999) found that 32% of the variance of species richness and approximately 40% of that of total abundance could be explained by spatial variations in habitat structure, but in this case the multiple regression models incorporated both substratum complexity (number of medium-sized boulders) and heterogeneity (percentage cover by *Posidonia*) (Fig. 2). Typically, target-organisms responded to variations in different descriptors according to their body size and life characteristics. For instance, benthic organisms and small sedentary fishes such as those in the spatial category 6 of Harmelin (1987) were positively associated with the number of small-sized holes and variations of rugosity (as a measure of micro-relief at 10^{-1}–10^{0} m), while larger, relatively mobile animals (e.g. demersal fishes) instead responded to the number of medium-to-large boulders inside each sampling unit (i.e. variations of complexity at 10^{1}–10^{2} m). On the other hand, the species data gathered in the hierarchical sampling programme described above (see Table 3) were accompanied by the measurement of several habitat descriptors, allowing a set of fish-habitat relationships which covers a large geographic range (~1000 km) at different spatial scales (from 10^{2} to 10^{4} m). As an example, the number of species seemed to be related to the number of medium-sized boulders and/or verticality, both considering all data together ($R^2 = 0.17$) (Fig. 3) and for four out of seven localities ($R^2 = 0.30 – 0.51$).

Habitat structure potentially determines the distribution and abundance of recruits. For instance, it appears that density of recently-settled (1.5–6 months) Mediterranean sparid fishes varies substantially amongst habitats, most individuals being found in water < 2 m deep but with distinct habitat associations (Harmelin-Vivien *et al.* 1995; Macpherson 1998). Thus the sparid *D. annularis* settles in seagrass beds, while *D. puntazzo, D. sargus* and *D. vulgaris* settlers are equally associated with gently-sloping sand, gravel, pebble and boulder substrata (Harmelin-Vivien *et al.* 1995). Labrid settlement is associated with macroalgae (Relini *et al.* 1994; Harmelin-Vivien *et al.* 1995).

Responses of fishes to variations in habitat structure outside of the Mediterranean

Other temperate regions have been studied to look for such relationships between habitat structure and fish assemblages at a local scale. Habitat descriptors apparently important in the spatial variability of fishes on rocky reefs include topographic complexity, depth, wave exposure, presence and abundance of macroalgae, and substratum type (Leum & Choat 1980; Jansson *et al.* 1985; Thorman 1986; Bodkin

1988; McCormick 1989; DeMartini & Roberts 1990; Norton 1991; Holbrook *et al.* 1992; Anderson 1994; Lowry & Suthers 1998). However, evidence of close relationships between habitat and particular demersal fishes has not always been found (e.g. Gillanders & Kingsford 1998). Extensive studies on fish-habitat relationships have been performed for coral reef areas in different geographic regions. The observed patterns include significant correlations between fish density and/or biomass and substratum complexity (Risk 1972; Luckhurst & Luckhurst 1978; Gladfelter *et al.* 1980; Roberts & Ormond 1987; Grigg 1994; McCormick 1994; McGehee 1994), coral reef zonation or habitat type (Alevizon *et al.* 1985; Galzin & Legendre 1987; Shpigel & Fishelson 1989; McClanahan 1994; Cadoret *et al.* 1995; Sluka & Sullivan 1996; Chabanet *et al.* 1997; Friedlander & Parrish 1998), depth (Smith & Saleh 1987; Coles & Tarr 1990; Greenfield & Johnson 1990; McGehee 1994; Friedlander & Parrish 1998), and proportion of live coral cover (Bell & Galzin 1984; Hourigan *et al.* 1988). As fish assemblages include a great variety of distinct ecological strategies, for example with respect to feeding habits, home ranges and reproductive behaviours, different habitat features are likely to influence each species or group of species (Jennings *et al.* 1996). When approached from a multiscaled perspective (e.g. Williams & Hatcher 1983; Russ 1984*a*, *b*; Bell *et al.* 1985; Findley & Findley 1985; Galzin 1987*a*; Williams 1991; Roberts *et al.* 1992; Galzin *et al.* 1994; Holbrook *et al.* 1994; Meekan *et al.* 1995; Ault & Johnson 1998), it is usual to find that different factors influence fish distribution at each scale; habitat features seem to be especially important for explaining differences at small-to-intermediate spatial scales. Interestingly, Ault and Johnson (1998), working on the southern Great Barrier Reef, found that the organization of fish communities on contiguous reefs appeared to be non-random and varied predictably with habitat, while changes on patchy coral reefs were largely unrelated to intrinsic habitat properties, suggesting that the relative importance of settlement and post-settlement processes in structuring fish assemblages may depend on the interaction between species' vagility and connectivity amongst sites. If reefs form a contiguous and heterogeneous habitat in situations similar to that of the Mediterranean, and species are able to migrate to areas that are favourable with respect to habitat characteristics and/or population density, then community structure should generally be more predictable. Both in temperate and tropical areas it is increasingly clear that differences in habitat help to explain the spatial variability of recruitment (Carr 1989; Doherty 1991; Levin 1991, 1993; Sale, 1991, 1999; Fowler *et al.* 1992; Planes *et al.* 1993; Caselle & Warner 1996; Steele 1997).

Benthic macroinvertebrates

Habitat selection by motile invertebrates subject to protection had seldom been studied in the Mediterranean, and there is only some evidence of habitat effects on density of urchins, lobsters and octopuses. Spatial heterogeneity, and especially the availability of shelters, may influence the distribution and the exposure of urchins to fish predators (Andrew 1993), so that where refuges are abundant, urchins can coexist with their predators, but at sites with low spatial heterogeneity and the same density of predators, urchins tend to be rare (Sala & Zabala 1996). Predation risk appears also to influence temporal variability of sea urchins, as their foraging behaviour is restricted to nocturnal hours when predation pressure is lower (Sala 1996).

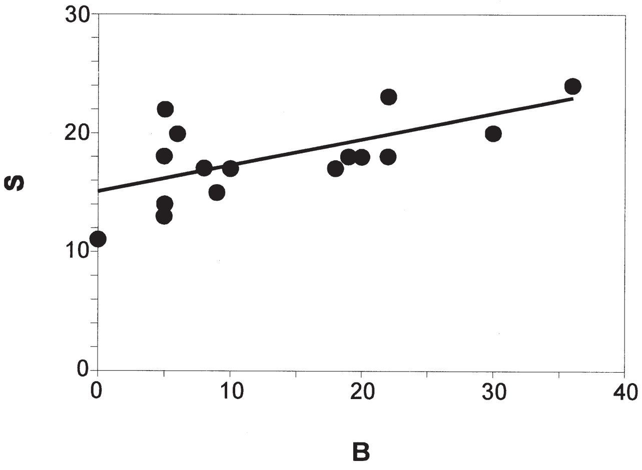

Figure 1 Relationship between number of fish species (S) and number of medium-sized boulders (B) per 250 m^2 transect in the rocky reefs surrounding the Cape of Palos (Murcia, SE Spain), showing the fitted Poisson regression curve $S = e^{(2.710+0.012\,B)}$ ($P < 0.05$), (the Poisson model is preferred because it is more appropriate for discrete variables with positive values) (from García Charton & Pérez Ruzafa 1998).

Laboratory and field experiments show a significant preference of the slipper lobster, *Scyllarides latus*, for shelters with more than one opening, with a small entrance close to the substratum, and for shelters in a horizontal position (Spanier & Shtayer 1992). Spanier and Shtayer (1992) also found strong tendencies for coexistence and sharing shelters with other conspecifics and moray eels. Díaz *et al.* (1999) observed in the Medes Islands Marine Reserve that spiny lobster (*Palinurus elephas*) juveniles settle into small holes in calcareous rock at 10–15 m depth, and that they move to crevices in the rock surface when reaching greater sizes.

Octopuses occur mostly on rocky reefs, but in many areas they are equally, or even more abundant, over sandy and muddy bottoms or in seagrass (Mangold 1983; Quetglas *et al.* 1998). Studies of small-scale space occupancy and temporal dynamics in *Octopus vulgaris* are scarce, probably because of the difficulty of observing the animals in the field due to their cryptic and nocturnal habits (Kayes 1974; Mangold 1983). An experimental study using artificial reefs in the Gulf of Mexico (Frazer & Lindberg 1994; Lindberg & Frazer 1994) showed that octopuses prefer widely-spaced units rather than

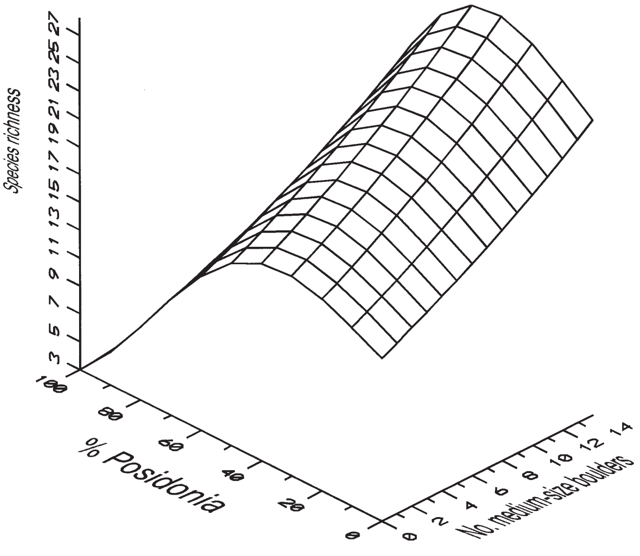

Figure 2 Fitted Poisson regression surface of the response of number of fish species per 50 m^2 to variations in the number of medium-sized rocky boulders and percentage cover by *Posidonia oceanica* in the rocky reefs off the Cape of Palos (Murcia, SE Spain) (García Charton 1999).

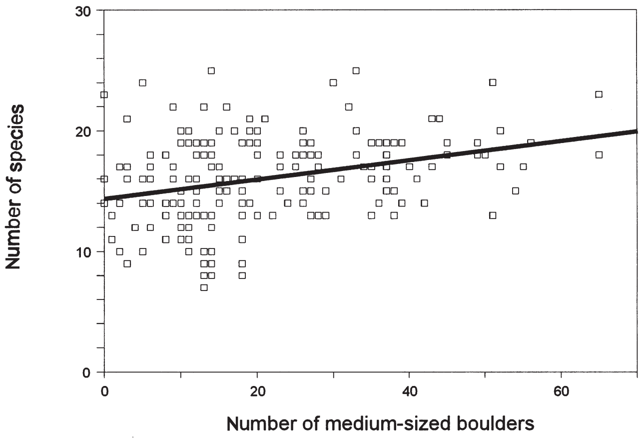

Figure 3 Relationship between number of fish species (S) and number of medium-sized boulders (B) per 250 m^2 for 189 sampling units censused across the Western Mediterranean (the localities sampled are indicated in Table 3), showing the fitted Poisson regression curve $S = e^{(2.70+0.004\,B)}$ ($P < 0.01$) (García Charton 1999).

aggregated ones, probably because more space amongst reef units provides a more favourable resource for mobile foragers by virtue of increased access to soft-bottom prey. Anderson (1997) showed that on rocky reef in north-eastern New Zealand *O. tetricus* preferred reef edge habitats and areas with high numbers of small boulders rather than flat reef habitats. However, there is some evidence that *O. tetricus* is associated with rocky reef habitats during the breeding season, whereas a considerable portion of its life is spent foraging on bivalves in soft sediment areas. Similar results were obtained for juveniles of *O. vulgaris* which occupied sheltered areas for a short time, but spent a longer period in larger homes and in areas where preferred preys were available (Mather 1994).

Effects of protection on habitat structure

Fishing activities sometimes exert direct effects on coastal ecosystems by altering, and even sometimes destroying, habitats (Ardizzone & Pelusi 1984; Jones 1992; Sainsbury *et al.* 1993; Accardo Palumbo *et al.* 1996; Sánchez Jerez & Ramos Esplá 1996; Martín *et al.* 1997). Therefore, cessation of fishing within MPAs may have positive effects by reducing or eliminating such impacts. On the other hand, intensive visitor usage of MPAs can lead to damage through increased trampling, breaking, mooring and harvesting of marine curios (Davis 1977; Moreno *et al.* 1984; Walker *et al.* 1989; Hawkins & Roberts 1992, 1993; Brosnan & Crumrin 1994; Wynberg & Branch 1997). There is some evidence of negative consequences of anchoring in *P. oceanica* meadows (Robert 1983; Porcher 1984; García Charton *et al.* 1993); anchoring may cause losses of structural complexity through reduced density and coverage, and may also impact primary production of the coastal meadows through reduced leaf lengths and areas in impacted zones. When diver impact on a coralligenous community of the Medes Islands MPA (NW Mediterranean) was monitored using the erect foliaceous bryozoan *Pentapora fascialis* as an indicator species (Sala *et al.* 1996), the mean size and density of *P. fascialis* colonies were greater at sites unused by divers than at those frequented by them. In the same location, similar results have been obtained for the gorgonian *P. clavata*, which appeared to suffer from higher mortality within frequented sites (Coma & Zabala 1994). At present, as pointed out by Sala *et al.* (1996), the general lack of information on the biology of most organisms in the coralligenous community makes it difficult to assess the response of this habitat to diver-disturbance. However, there is little doubt that the increasing number of divers, especially within Mediterranean MPAs, has the potential for considerable negative impacts in the near future.

Concluding remarks

Habitat structure is likely to drive a large part of spatial variability in the distribution and abundance of Mediterranean target organisms, especially when abundance is assessed at small spatial scales. Furthermore, habitat structure is likely to influence the strength of protective measures, either reinforcing or buffering the expected effects of establishing MPAs. Thus, distinguishing the relative contribution of habitat structure can help to elucidate the actual effects of protection. As stated by Jennings *et al.* (1996), 'the inclusion of a procedure to collect basic habitat data provides a useful approach for reducing the unexplained variance in biomass estimates and improves the probability of elucidating the effects of other factors on the distribution and biomass of (...) reef fishes'.

Actually, there are few hard data with which to characterize relationships between Mediterranean target species, either invertebrates or fishes, and habitat. From a species-oriented perspective, the problem of the influence of habitat is equivalent to understanding how target organisms use (and perceive) their environment. The solution to this problem rests on answering a series of questions. What features of habitat are influencing the species of interest, and how might these features be measured? What is the relevant scale at which habitat is important for particular species? What mechanisms underlie observed patterns, including food supply, shelter for recruits and/or adults, and availability of substratum for spawning or nesting?

To address these objectives, more functional or process-oriented studies have to be undertaken, moving from correlative to manipulative sampling designs. On the other hand, differences in the species-habitat relationship from site to site and through time are likely to occur, thus leading to the need for long-term studies in a variety of Mediterranean localities. MPAs are excellent natural laboratories in which to face these problems. Protective activities, while diminishing impacts such as habitat destruction by fishing gears, can increase other potential problems through increased visitation. Management of Mediterranean MPAs should therefore incorporate measures to mitigate such effects.

Conclusions and perspectives

This paper raises the problem of whether current studies in the Mediterranean Sea permit us to understand or predict the consequences of the establishment of MPAs. From the preceding review a series of methodological concerns emerges. To improve understanding of the mechanisms operating in MPAs, sound sampling designs are needed, and these should (1) generate long-term data sets, (2) be based on wide-scale comparisons of a number of protected and unprotected localities, (3) include multi-scaled perspectives both in space and time, and (4) control for factors other than protection (e.g. in the physical environment) that are likely to influence the spatio-temporal variability of exploited populations. In this way, a number of questions might be addressed. What does 'long-term' mean? How can the scales relevant to studies be selected? What are the important features of habitat to consider, and how may they be measured? How can the natural variability of measured variables be introduced into analytical procedures in order to pick out the actual effects of protection? On the other hand, to perform accurate predictions it is necessary to (1) understand and quantify the mechanisms underpinning the observed patterns, and (2) develop the appropriate modelling tools. Therefore, more experimental work is needed to feed the models to be built.

The recent developments of environmental impact assessment techniques (Green 1979; Hurlbert 1984; Stewart-Oaten *et al*. 1986; Underwood 1992; Wiens & Parker 1995; Schmitt & Osenberg 1996), based on field experimental designs and analysis of variance, aimed at statistically differentiating the effect of human interventions from the natural multiscaled variability of ecosystems, can be applied to the problem of effects of MPAs considering explicitly their multiscaled nature in space and time. These experimental designs (mensurative *sensu* Hurlbert [1984]) involve making measurements at one or more points in space or/and time, where the effects of an external imposition such as protection of a certain area are checked with reference to several control areas, and considering other environmental factors such as the type of habitat, depth and season. Here the statement of an appropriate hypothesis is crucial for the correct interpretation of results. Also, because the detection of significant differences in fish population when these differences actually exist is important in environmental management, the power of the analysis has to be considered (Peterman 1990; Fairweather 1991), especially when fish population data are very similar amongst treatments. The lack of a correct pattern of spatial and temporal replication, or the use of data for testing a treatment effect (e.g. differences in fish abundance between a MPA and unprotected area) with an error term inappropriate to the hypothesis being considered, confounds the interpretation of results (Hurlbert 1984; Underwood 1997). Generally, in these mensurative experiments, pseudoreplication is often a consequence of the influence of spatial variation in habitat (García Charton 1999), or follows from the fact that actual physical space over which visual counts are performed is smaller or more restricted than the inference space implicit in the hypothesis being tested (Hurlbert 1984). For these reasons, we argue that it is better to consider a nested design so that an appropriate level of spatial replication can be included (García Charton & Pérez Ruzafa 1999). Increase in the number of samples, and/or spatial replication with nested factors, ameliorates the chances of correctly interpreting the observed spatial heterogeneity of fish population at different spatial scales (Andrew & Mapstone 1987; Clarke & Green 1988).

Other insights into the effects of MPAs could emerge from the application of 'terrestrially-based' landscape ecology (Urban *et al*. 1987; Turner 1989) to coastal marine ecosystems (Steele 1989; Fairweather & Quinn 1992; Jones & Andrew 1992; Robbins & Bell 1994; but see Haslett 1994). This approach is based on the explicit recognition of the hierarchical nature of habitat structure (Kotliar & Wiens 1990), so that it is possible to conceptualize the observed pattern and the associated processes in spatially-explicit terms, differentiating amongst processes occurring at different spatial (and temporal) scales, and elucidating the linkages amongst habitats and amongst scales. Examples of how to use such a perspective in the marine environment are provided by Bell *et al*. (1995), Irlandi *et al*. (1995), Garrabou (1997), Vidondo *et al*. (1997) and García Charton *et al*. (1999). Other approaches include those of metapopulation (Hanski 1994; Hanski & Gilpin 1997) and 'sources-and-sinks' theory (Pulliam 1988; Lewin 1989; Pulliam & Danielson 1991). Both are based on spatially-explicit modelling, in which populations are viewed as formed by local subpopulations inhabiting spatially distinct habitat patches, and characterized by local extinction and colonization rates. For instance, Man *et al*. (1995) used a metapopulation model to investigate the influence of management decisions about MPAs as tools that are capable of enhancing recruitment into fished patches, and thus preventing fishery-target depletion. Carr and Reed (1993) and Allison *et al*. (1998) have presented applications of the 'source-and-sinks' concept to MPAs, opening ways to provide hypotheses to be tested by field experiments.

Solutions to these methodological concerns for evaluating the ecological effects of Mediterranean MPAs, especially the aspects relating to habitat and scale, would give us some additional clues to improved management decision-making. For example, how big should a Mediterranean MPA be? What proportion of coastal area should be protected? Is it better to protect a few large rather than a lot of small marine areas? What habitats have to be included in a Mediterranean MPA to be effective? The issues addressed here are probably those that every ecologist should be concerned by, but they have seldom been discussed within the framework of Mediterranean MPAs. It is time to ambitiously face their study with an adequate level of coordination amongst research groups, to reach common objectives, hypotheses to be tested, sampling programmes, field methods and discussion of data.

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