Mini-review

Ecological heterogeneity and the evaluation of the effects of marine reserves

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Received 15 June 1998; received in revised form 22 February 1999; accepted 5 May 1999

Abstract

In recent decades marine reserves have been established throughout the world as a management tool for compensating the effects of overfishing on coastal marine stocks. Despite the growing literature about the expected response of populations and communities to protection from fisheries, and the number of studies measuring some of these effects, most of the mechanisms supposed to work in a marine reserve have not yet been empirically demonstrated. One of the main difficulties ecologists have to face when approaching this problem is the inherent spatial and temporal heterogeneity of ecosystems. This paper reviews the relevant literature and addresses the influence of physical environment (or habitat structure) on ecological processes occurring at the individual, population, and community / ecosystem levels of organization. It evaluates how the responses confound the ''reserve effect'' with some aspect of the ''habitat effect''. Finally, it proposes some practical considerations for improving the methods aiming to evaluate the effect of protection in the face of heterogeneity, illustrated with some examples taken from our studies on Mediterranean rocky reef fish assemblages, and argues that a multiscaled, hierarchical approach to this problem (the seascape perspective) should be adopted as an integrating principle when designing a research program aiming to understand the way marine reserves work as fisheries management tools. © 1999 Elsevier Science B.V. All rights reserved.

1. Introduction

At present it is widely acknowledged that a great proportion of the world's marine fish stocks are over-exploited (Lauck et al., 1998). Marine reserves (≡protected areas ≡ harvest refugia) have been strongly advocated as an ideal tool for the management of coastal fisheries (Plan Development Team, 1990; Roberts and Polunin, 1991; Dugan and Davis, 1993; Agardy, 1994), and, consequently, they have been established throughout the world. When protecting a marine area we stop (or reduce) fishing pressure, at the same time as regulating other human activities. A large literature has developed hypotheses about the expected response of individuals, populations, communities and ecosystems to the establishment of marine reserves (Plan Development Team, 1990; Roberts and Polunin, 1991; Jones et al., 1992; Carr and Reed, 1993; Jennings and Polunin, 1996; Allison et al., 1998). Several studies have characterized some of

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the local responses of marine communities to protection from fisheries (e.g., Bell, 1983; García Rubies and Zabala, 1990; Polunin and Roberts, 1993; Francour, 1994; Dufour et al., 1995; Harmelin et al., 1995; Jennings et al., 1996a; Rakitin and Kramer, 1996; Russ and Alcala, 1996).

However, most of the mechanisms supposed to work in a marine reserve have not yet been empirically demonstrated. One of the difficulties of achieving this task is that these mechanisms (see Plan Development Team, 1990) are subjected to confounding with other causal processes not directly related to protection. In effect, the forces that drive the spatial and temporal variation in community structure (species composition and richness, relative species' abundances, trophic organization, size structure, etc.) can be both physical (habitat structure, light and nutrient availability, currents and wave exposure,...) and biological (recruitment, predation, competition, mutualism, disturbance,...) in nature. Thus, the problem rests on determining the relative importance of such processes in influencing community structure (Menge and Farrel, 1989). The understanding of how marine reserves work as a management tool has to be gained in this framework. On the other hand, research on patterns and the causal processes behind them will emerge from a collection of studies performed at different sites, because only by this means will we achieve the adequate number of replicates for the different treatments (namely protection vs. non-protection) to be compared, so that it will be possible to find evidence of the effects of treatments over natural variability (the problem of the statistical power of field experiments) (Sale, 1984; Peterman, 1990; Fairweather, 1991; Underwood, 1997). But when any attempt is made, via natural experiments, to distinguish between the effect of protection from fisheries and natural variability, a problem arises which is associated with the inherent spatial and temporal heterogeneity of ecosystems (see Kolasa and Pickett, 1991, for a comprehensive review). Only by explicitly incorporating heterogeneity in such analyses can we avoid the possibility of confounding the effects of treatments with those of uncontrolled natural factors – the problem of 'pseudoreplication' *sensu* Hurlbert (1984).

The present article aims to approach the problem of confounding by reviewing how the heterogeneity of ecosystems adds complexity to the processes acting behind the effects of protection on marine populations and communities, and consequently to the methods to be developed for evaluating and understanding these effects. Most of the concepts are illustrated with the case of littoral fish assemblages, which are directly affected by protection.

2. Ecological heterogeneity

Only recently, ecologists have been aware of the importance of spatial and temporal heterogeneity of ecosystems for understanding ecological processes (Levin, 1992). We can intuitively define heterogeneity as the multiscaled spatial and temporal patterning of organisms and the environment in which they live. In our search for pattern, scale has not to be considered an intrinsic property of the process to be studied, but rather a methodological decision we must take as observers, keeping in mind that most of the ecological processes are multiscaled in nature (Giller and Gee, 1987; May, 1989; Wiens, 1989; Allen and Hoekstra, 1991; Levin, 1992). Heterogeneity has a potential role in modifying the consequences of ecological processes (Wiens, 1976; Levin, 1992; Oksanen et al., 1992), thus influencing the way species coexist in space and time (Downing, 1986), or how they are organized in trophic webs (Schoener, 1989; Polis and Strong, 1996). The consideration of heterogeneity has a crucial influence on the construction of ecological models (Levin, 1976; Kolasa, 1989; Hastings, 1990), the design of field experiments (Dutilleul, 1993), and the management of natural resources (Loehle, 1991; Usher, 1991).

The patterning of ecosystems is a result of the interaction between the variation of environmental constraints and the differential responses of organisms to these constraints (Milne, 1991). Therefore, we can distinguish between the heterogeneity imposed by the spatial and temporal change of the environment, and the variability emerging as a result of biological processes (species interactions, dispersal, colonization, stochastic temporal variation,...) (Ives and Klopper, 1997). In the discussion below, we will concentrate on the external heterogeneity, i.e., that imposed by the variation of environmental factors. More specifically, we are interested on the influence of

the physical environment, what Bell et al. (1991) called ''habitat structure'', which can be source of confounding when measuring the effect of protection.

3. Habitat structure and ecological processes

Following Bell et al. (1991) we can define habitat structure as 'the physical arrangement of objects in space'. McCoy and Bell (1991) focused this definition by establishing a set of criteria for recognizing habitat structure, namely that a functional interaction between habitat structure and the organism of interest must be demonstrated, and the scale of study must be suitable to the organism of interest. Moreover, they proposed a graphical model of habitat structure, deciding that three axes could encompass the breadth of ecological relationships implied by 'habitat structure' and related terms: heterogeneity, complexity, and scale, which could be respectively, attributed to the horizontal and vertical components of the structural habitat, and the total area (or volume) used to measure heterogeneity and complexity. The problem is then to ascertain the relative importance of habitat structure (which has a functional effect) on the organism to be studied. For clarity, we have structured the discussion distinguishing between processes occurring at different levels of organization, from the individuals and populations belonging to species of commercial interest (with special mention to the processes involving the pelagic phase of the life-cycle of these species), to the community / ecosystem level.

3.1. Individual-to-population processes

At the individual level we are concerned with behaviour (Lejeune, 1984; Polunin and Klumpp, 1989; Jan and Chang, 1993), physiology (Taborsky and Limberger, 1980; Kotrschal, 1983; McFarland, 1986; Boujard and Leatherland, 1992), and morphology (Anderson, 1990; Turingan et al., 1995; Wainwright and Richard, 1995) as aids to understanding how individuals, that are constrained by their body structure (Schoener, 1989), select the food items, partition the substrate for spawning, or escape from predators, adverse environmental conditions and fishing pressure in the presence of small-scale spatial variation of habitat. At the population level, we are

interested in habitat selection of the different species in a patchy environment (e.g., Anderson, 1994; Sluka and Sullivan, 1996; García Charton et al., in press).

Thus, at this level, habitat structure could offer a mechanistic basis (Schoener, 1986; Inchausti, 1994) for explaining small-scale spatial and temporal patterns in communities, by understanding how individuals and species select and use a particular set of patches. The spatial arrangement of habitat could then help to explain niche overlap or resource partitioning in more spatially explicit terms. On the other hand, it has become increasingly clear that it is impossible to model the trajectories of change in numbers with time without considering the patchiness of nature and individual behaviour, specifically taking into account the non-linearity of movement patterns and reproductive behaviour of such individuals (Wiens, 1976; Schoener, 1986; May, 1989). Obviously, all these studies have to be performed at the appropriate scale (Morris, 1987).

3.2. Recruitment

Extensive studies on recruitment of fishes in coral reefs, which is accepted as having a critical role in determining fish population structure (see review by Booth and Brosnan, 1995) have demonstrated that the extremely variable nature of this process both in space and time (at different scales) is closely related to changes of habitat structure (Doherty, 1991; Sale, 1991, 1999; Fowler et al., 1992; Planes et al., 1993; Caselle and Warner, 1996). Effect of habitat structure on recruitment of temperate reef fishes is receiving growing attention (e.g., Carr, 1989, 1994; Levin, 1991, 1993; Harmelin-Vivien et al., 1995; García Rubies and Macpherson, 1995; Steele, 1997; Macpherson, 1998), while a few studies have considered the influence of protection on recruitment of exploited populations (e.g., Macpherson et al., 1997). Several studies have explored the interplay between recruitment variability and dynamics of reef fisheries (e.g., Richards and Lindeman, 1987). The study of the processes acting at the younger stages of reef populations (dispersal, settlement, recruitment) must incorporate such a habitat-based, multiscale approach to be able to understand and, if possible, predict their vagaries and, in this way, to be useful for taking decisions on management (Hughes et al., 1999).

3.3. Community structure/ecosystem processes

Traditionally, ecological communities have been viewed as a set of species that differ in their distribution and relative abundance (the structural approach) (Strong et al., 1984), or alternatively as an ecosystem of interacting elements (the functional approach) (Pomeroy and Alberts, 1988). In both approaches, spatial heterogeneity / habitat structure have a crucial influence.

Habitat structure has often been related to fish assemblage structure (species composition and richness, and relative abundances) at a local scale: substrate complexity (Luckhurst and Luckhurst, 1978; Pérez Ruzafa, 1989; Norton, 1991; Holbrook et al., 1992; Grigg, 1994; Macpherson, 1994; McClanahan, 1994; McCormick, 1994; McGehee, 1994; Jennings et al., 1996b; Chabanet et al., 1997; Ault and Johnson, 1998; Friendlander and Parrish, 1998; García Charton et al., in press), coral reef zonation (Alevizon et al., 1985; Galzin and Legendre, 1987; Letourneur and Chabanet, 1994; Meekan et al., 1995), live coral cover (Bell and Galzin, 1984), type and size of drifting objects (Safran and Omori, 1990; Druce and Kingsford, 1995; Kingsford, 1995), kelp density (Bodkin, 1988; DeMartini and Roberts, 1990), variations of seagrass canopy (Bell and Westoby, 1986; Bell et al., 1988; Connolly, 1994), and even small-scale hydrodynamic patterns (Kingsford and Choat, 1986; Ayvazian and Hyndes, 1995). Such spatial patterns are evident at different from local to biogeographic-scales (Russ, 1984a, b; Williams, 1991; Bell et al., 1985; Galzin, 1987a; Findley and Findley, 1989; Roberts et al., 1992; Galzin et al., 1994; Meekan and Choat, 1997). The point here is that the influence of habitat structure interferes with the effects of protection, and then the 'reserve effect' on community structure has to be investigated in combination with spatial variation of habitat at a multiscale perspective to avoid confusion.

The interactions among species belonging to a community can be studied from different perspectives. Particular emphasis has been placed on predator–prey relationships and competition. Habitat structure introduces a factor of environmental heterogeneity to both processes, either on predation by facilitating predator avoidance (Savino and Stein, 1989; Nelson and Bonsdorff, 1990; Kingsford, 1992; Oksanen et al., 1992;

Hixon and Beets, 1993; Irlandi, 1994; Connell, 1996; Lancaster, 1996; Beukers and Jones, 1997), or on competition by facilitating co-existence (Wiens, 1977; Choat and Bellwood, 1985; Tilman, 1994; Ives, 1995). Special mention could be made of the incidence of parasitism related to protection of marine areas (Sasal et al., 1996, 1997), where perhaps the influence of habitat structure on the transmission of parasites is still a neglected factor (Sousa and Grosholz, 1991).

There have been numerous studies on the role (direct, or mediated by indirect effects *sensu* Wooton, 1994) of fish and sea-urchin feeding in structuring benthic communities (e.g., Choat, 1982; Lewis, 1986; Morrison, 1988; Andrew and Jones, 1990; Hay, 1991; Jones et al., 1991; Leinaas and Christie, 1996; Miller and Hay, 1996). These considerations have inspired the idea of the "cascade effect" of protection (Jones et al., 1992; McClanahan, 1994; Sala and Zabala, 1996; Sala, 1997). Several of these studies have focused on the influence of habitat structure and scale in such relationships (Diehl, 1992; Andrew, 1993; McClanahan, 1994; McCormick, 1995; Hixon and Brostoff, 1996; Sala, 1996). Spatial variation of habitat introduces complexity to the study of trophic interactions (Livingston, 1984; Schoener, 1989; Schneider, 1997). In this sense, it seems unwise to discuss solely linear "cascade effects" of protection (for instance, as conceptualized by Jones et al., 1992) i.e., directly conferring predominance to the "top–down" or predator-controlled processes, against "bottom–up" (resource-controlled) ones, when it appears progressively clearer that both "bottom–up" and "top–down" processes can jointly determine community structure (Hunter and Price, 1992; Menge, 1992; Power, 1992; Strong, 1992; Leibold et al., 1997). Ecologists should better ask "How do bottom-up and top-down effects interact and influence each other?" and "What are the mechanisms underlying variation in each?" (Menge, 1992). This is even clearer if we take the intrinsic complexity of food webs into account (Polis and Strong, 1996).

4. Temporal dynamics

The study of temporal variability in community structure is of primary concern for the evaluation of

the "reserve effect" on ichtyofauna. In fact, several studies attempting to quantify the effectiveness of marine reserves focused on in situ differences among years (e.g., Francour, 1994; Dufour et al., 1995). The temporal variability of fish assemblages has been the object of a number of studies, considering different scales: day–night (Colton and Alevizon, 1981; Nash, 1986; Howard, 1989; Wright, 1989), lunar (Letourneur, 1992), seasonal (Clements and Choat, 1993), pluriannual (Brock et al., 1979; Ebeling et al., 1980; Galzin et al., 1990; Sale et al., 1994), or multiscale (Galzin, 1987b; Gibson et al., 1996). Some studies focused on the changes following a disturbance (Walsh, 1983; Williams, 1986; Letourneur, 1991; Chabanet et al., 1995). Other studies paid attention to coupled spatio-temporal patterns (Jansson et al., 1985; Choat et al., 1988; McCormick, 1989; Robertson and Duke, 1990; Fowler, 1990; Holbrook et al., 1994; Wantiez et al., 1996). As previously mentioned, recruitment is a temporally (as well as spatially) variable, multiscaled process (Williams, 1983; Warner and Hughes, 1988; Doherty, 1991; Caselle and Warner, 1996). Analogously, ecosystem processes are temporally variable at multiple scales (Shugart and Urban, 1988).

All this temporal variability can obscure the detection of the effects of protection. Furthermore, a relationship between spatial and temporal scales of variation is evident for ecological processes (Giller and Gee, 1987; Steele, 1989; Wiens, 1989; May, 1989; Levin, 1992). This coupling leads to methodological constraints, due to the fact that spatial variability interacts with temporal trends (Thrush et al., 1994; Stewart-Oaten et al., 1995; Underwood, 1997). Another point is that long-term variation has to be distinguished from small-scale temporal fluctuations (Wolfe et al., 1987; Overton and Stehman, 1996; Thomas, 1996), in order to ascertain the magnitude and importance of changes.

5. Seascape ecology

As shown above, consideration of ecological heterogeneity in relation to protection of marine areas, inevitably leads to several interrelated topics: habitat (spatial variation), change (temporal variation), and scale. We have seen how these themes must be considered under a functional view, and from a species-oriented perspective. Furthermore, all these aspects act from the individual to the community / ecosystem level of organization. Moreover, when we intend to reach the desired link between species and ecosystem perspectives, the topics of environmental heterogeneity and spatio-temporal scale recurrently emerge as integrating factors – see the volume edited by Jones and Lawton (1995). Heterogeneity is a crucial factor when building models, designing field experiments, and managing natural resources. In order to describe, evaluate and manage the effectiveness of marine reserves, we must take all the different aspects of heterogeneity into consideration. What we need is a conceptual, as well as methodological framework for dealing with heterogeneity.

In the last decade, landscape ecology has been developed as an allied set of concepts, theories and tools for studying the ecological scale-dependent effects of the spatial patterning of ecosystems (Urban et al., 1987; Turner, 1989). Under a landscape perspective we have to identify relevant scales (Wiens, 1989), recognize habitats at each scale (e.g., Knight and Morris, 1996), and detect functional links among habitats and among scales (Dunning et al., 1992), in order to explain spatio-temporal pattern. This approach is based on the explicit recognition of the hierarchical nature of patch structure (Kotliar and Wiens, 1990). Components of a hierarchical system are organized into levels according to functional scales. Landscapes have a special kind of between-levels structure: they are nested spatially, so that the hierarchical levels are often evident as patches in nature (Urban et al., 1987; Turner, 1989). Each hierarchy has to be constructed in relation to a specified phenomenon of interest (e.g., see the hierarchical concept of disturbance presented by Pickett et al., 1989), by means of non-arbitrary, operational methods (Wiens, 1989). Processes occurring at the individual (Morris and Brown, 1992), population (e.g., Knight and Morris, 1996) or community / ecosystem (e.g., Polis et al., 1997) levels can be viewed under this landscape perspective. Temporal change has also to be studied from this multiscale, hierarchical view (Rahel, 1990). Some related topics are those of source-sinks (Pulliam, 1988; Lewin, 1989; Pulliam and Danielson, 1991; Brawn and Robinson, 1996), metapopulations (Hanski, 1994; Hanski and Gilpin, 1997), and the

relationship between local abundance and regional distribution (Maurer, 1990; Gaston and Lawton, 1990; Lawton, 1993; Caley and Schluter, 1997).

Marine systems have often been considered under a multiscale perspective (e.g., Dayton and Tegner, 1984; Barry and Dayton, 1991), but only recently have attempts been made to apply the ''terrestrially-based'' landscape perspective to marine habitats – the seascape perspective (Steele, 1989; Jones and Andrew, 1992; Fairweather and Quinn, 1992; Robbins and Bell, 1994; Bell et al., 1995; Irlandi et al., 1995; García Charton et al., in press, but see Hasslett, 1994). Other studies have focused on functional linkages among habitats (frequently presenting fish as vectors), as ways marine seascapes promote heterogeneity (Parrish, 1989; Fairweather and Quinn, 1992; Bell and Worthington, 1992; Gillanders and Kingsford, 1992; Caley, 1995; Irlandi and Crawford, 1997; Polis et al., 1997). Marine organisms and habitats forming the littoral seascape are particularly suitable for applying such an approach, since habitats show an evident and easily recognizable multiscaled patchiness, and species generally present such a bipartite life-cycle, home-range and mobility, to allow them to experience processes acting at several, simultaneous spatial and temporal scales.

6. Examples from Mediterranean rocky reef fish assemblages

In recent years we have undertaken the study of the spatial and temporal variability of Mediterranean rocky reef fish assemblages, in an attempt to take the hierarchical nature of marine habitats into account, using visual censuses by SCUBA as survey technique. These studies were done in the rocky shores along the 140 km of the coast of Murcia (SE Spain) (Fig. 1). The bottom in these areas is formed by a mosaic of rocky substrate interspersed with extensions of sand and gravel, and clumps of *Posidonia oceanica* meadows. Two complementary research strategies could be used for studying spatial pattern and fish-habitat relationships (García Charton et al., in press): to work at a continuous range of spatial scales, or to adopt a simultaneous multiscale perspective. The first approach implies the use of statistical procedures for spatial pattern analysis (Upton and Fingleton, 1985; Galzin and Legendre, 1987; Legendre and Fortin, 1989; García Charton et al., in press). The principle of the second approach is to compare patterns among several (arbitrarily) selected points on the scale spectrum (e.g., Galzin, 1987a; Morrisey et al., 1992; Lindegarth et al., 1995; Underwood and Chapman, 1996; García Charton et al., in press), and to identify relevant scales by exploring data simultaneously through hierarchical (nested) analysis of variance (Underwood, 1997).

6.1. Spatial pattern at local scale: transect of contiguous quadrats

6.1.1. Sampling design and analysis of data

This study took place on the rocky reefs surrounding the Cape Palos (Murcia, SE Spain, 37°38′N, 0°42′W) (Fig. 1). To examine the spatial pattern of fish assemblage at a local scale, during the summer of 1992 we performed visual censuses on 140 contiguous 50 m^2 quadrats along a 1400 m transect (Fig. 1), thus covering scales ranging from 10^1 to 10^3 m. We deployed the transect by consecutive segments extending a 200 m long ballasted rope, which was marked every 10 m (by adhesive coloured tape) to delimit the quadrats. Every segment was placed in a random order to prevent a coupling between its position along the transect and time of sampling. The transect followed the 10 m isobath as close as possible to avoid the influence of depth, and we performed visual censuses as explained by García Charton and Pérez Ruzafa (1998).

Spatial pattern of fish assemblage was quantified in three ways: (1) Spatial correlograms with Moran's I as autocorrelation statistic (Upton and Fingleton, 1985; Legendre and Fortin, 1989; Legendre, 1993), using the program AUTOCORRELATION included in the 'R' v.3 package (Legendre and Vaudor, 1991). We tested the null hypothesis that the autocorrelation statistic is not significantly different from zero with a probability level of 5%, after the overall significance of the correlogram has been determined checking whether it contains at least one value which is significant at the $0.05 / 139 = 0.00036$ Bonferroni's corrected level for multiple tests (Legendre and Fortin, 1989). (2) Mantel tests, performed with the MANTEL v.3 program included in the 'R' package. In short, the Mantel statistic is the sum of the cross-products of the corresponding dis-
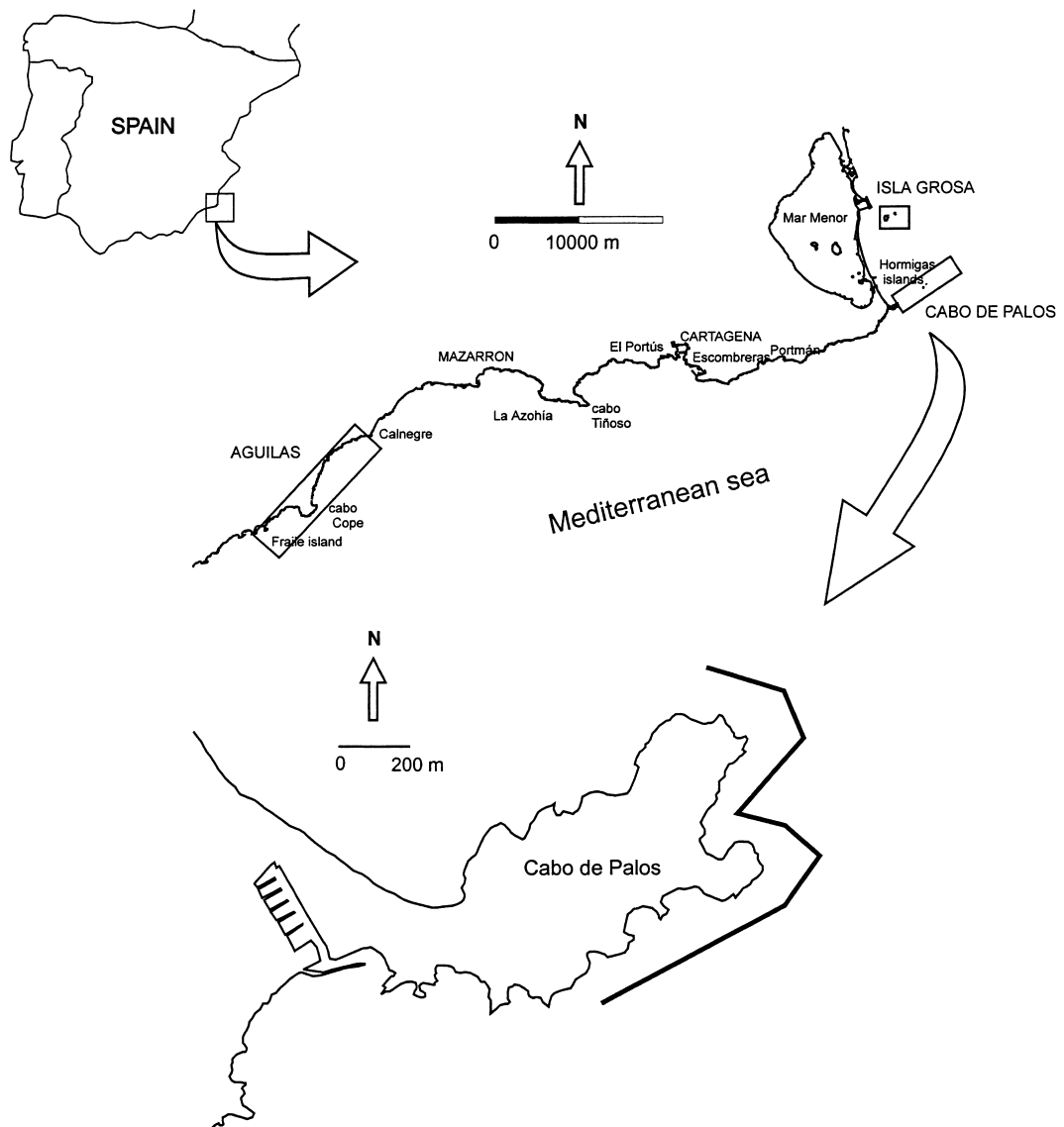
Fig. 1. Map of the coast of Murcia (SE Spain), indicating the location of the three localities at which hierarchical sampling were performed, and the transect (solid line) located in the Cape Palos.

tances in two matrices (Legendre, 1993). We computed the normalized Mantel statistic r (which takes values from -1 to $+1$), which was tested for significance through a permutation test at the 0.001 level (i.e., performing 999 permutations of the original matrices), under the null hypothesis that both matrices are not linearly related (Legendre and Troussellier, 1988). We looked for a spatial trend in the matrix of biological data, computing Mantel's r between a matrix **A**, constructed with the Steinhaus coefficient of similarity among all pairs of quadrats for the species abundance data (Legendre and Legendre, 1983), and a matrix **B** of geographic distances among quadrats on the transect; by calculating the Mantel statistic r between these two matrices, we wish to determine whether the ecological similarity decreases as the

samples get to be spatially farther apart, i.e., if there is a spatial gradient in the multivariate ecological data. We used also this normalized Mantel statistic in the univariate case, calculating r between the matrix **B** of geographic distances and each one of the matrices of similarity among pairs of quadrats constructed the unsigned difference between the values of the assemblage variables in each quadrat. (3) Mantel correlograms (Legendre and Fortin, 1989) for the above mentioned matrix **A**, looking for a significant spatial pattern for multivariate data. Each value of the normalized Mantel statistic against distance classes was tested for significance using Mantel's normal approximation (Legendre and Fortin, 1989), after carrying out a global test using the Bonferroni's method (as above).

6.1.2. Results

A total of 45 species belonging to 19 families were recorded throughout the study, and thus included in the analyses. Labridae (12 spp) and Sparidae (10 spp) were the families that contribute most to the species richness. Mean species richness was 11 (±0.3 SE) species 50 m^{-2}, with values varying between 4 and 20 species per quadrat. Mean total abundance was 66.5 (±4.4 SE) individuals 50 m^{-2}, this number ranging from 10.4 to 362.2 fish per quadrat.

All the correlograms pass the Bonferroni's test of overall significance, since $p < 0.00036$ at least for one of the individual values of I (generally for the first distance classes). Further examination of correlograms shows that, as expected, observations located near one another have very similar values (there is significant positive autocorrelation at low distance classes for all variables) (Fig. 2). But the relevant observation here is that, generally, there is significant (positive or negative) autocorrelation at more than one spatial scale, revealing the existence of spatial patterning for the biological variables measured on the quadrats. Total abundance shows a significant negative peak at distance class 9 and its respective positive peak at distance class 18 (Fig. 2). This structure corresponds to a patchy distribution of this variable in space (Legendre and Fortin, 1989), with a patch size
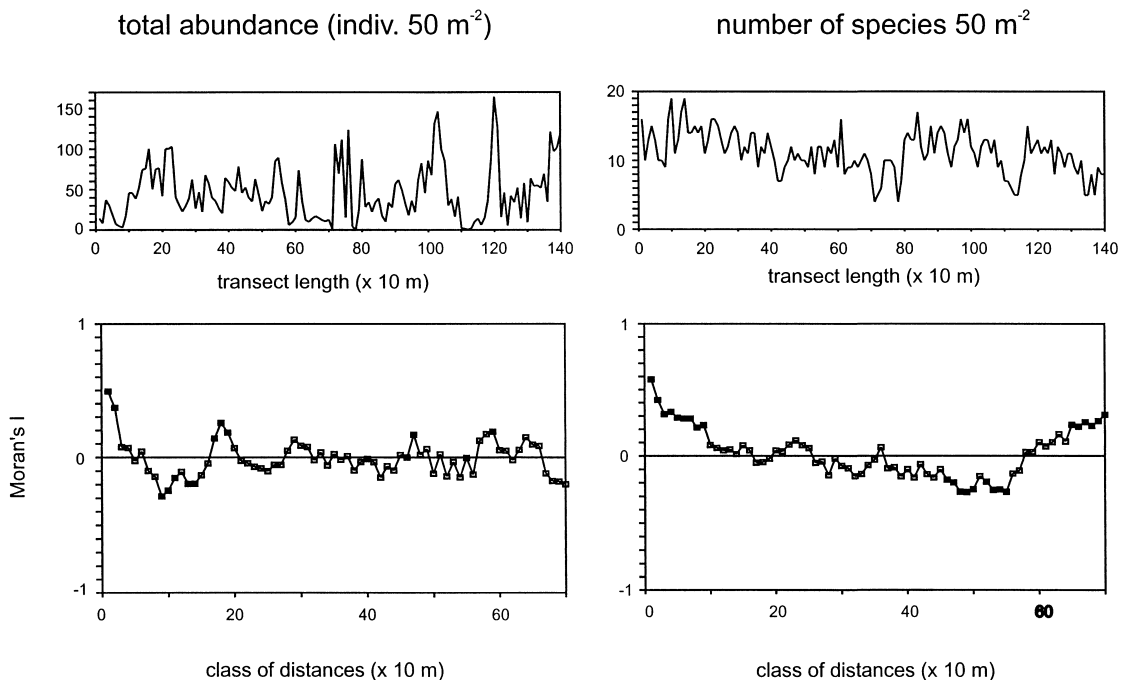

Fig. 2. Number of individuals and number of species of fish per quadrat in 140 consecutive quadrats along the continuous transect performed at Cabo de Palos (Murcia, SE Spain) (top), and corresponding serial autocorrelation between pairs of quadrats separated by distances from 1 (adjacent quadrats) to 70 (half the length of the transect) (down); (■) significant values, (□) non-significant values.

of 180 m along the transect. This variable also presents a second positive peak (distance class 47), probably as a reflection of the same pattern detected above. Species richness shows a correlogram which is characterized by significant positive values at low distance classes, followed by high negative values of I between 460 and 550 m, with a peak at distance class 49, and again positive autocorrelation for distance class 70 (Fig. 2). This could be reflecting a gradient, or a situation of a few distinct regions along the transect of similar values for species richness (Legendre and Fortin, 1989). Both patterns (small-scale patchiness of total abundance; larger scale or gradient, for the species richness) seem easy to be recognized when we inspect the actual values of these variables along the transect (Fig. 2).

The Mantel statistic r computed between the matrix of differences among individual values of species richness and the matrix **B** of geographic distances among quadrats was significant ($r = 0.132$, $p < 0.001$), detecting the existence of a spatial gradient (notice that the correlogram computed on this variable depicted the same situation). On the other hand, the Mantel test between the matrix **A** calculated on the species data, and the matrix **B** of geographic distances did not exhibit any spatial trend ($r = -0.006$, $p = 0.43$). So, we must accept the null hypothesis and reject that there is some spatial gradient along the transect for the fish assemblage as a whole (i.e., taking both species composition and relative abundance into account). Also, after computing the Mantel correlograms for matrix **A**, there was neither overall significance (at the Bonferroni-corrected level $p < 0.00036$) nor any significant individual of Mantel's r found for species data. So, it was not possible to detect any spatial patterning for multivariate data.

6.2. Spatial pattern at larger spatial scales: hierarchical sampling design

6.2.1. Sampling design and analysis of data

During the summer of 1996 we selected three localities (L) along the coast of Murcia (Cabo de Palos, Isla Grosa, Aguilas) (Fig. 1). These localities represents a variety of environmental features (underwater topography, oceanographic conditions, fishing pressure, frequentation by divers, etc.). Then we randomly selected three sectors (S) within each locality,

three zones (Z) within each sector, and within each zone we performed three replicate 50×5 m transects (T). This sampling effort makes a total of 81 samples, and incorporated four spatial scales (Fig. 1), ranging from 10^1 m between replicate transects to 10^4 m between localities. The only conditions for locating the transects were to maintain a homogeneous depth (10–12 m), and that the bottom type had to be predominantly rocky. For performing visual censuses we followed basically the technique used by García Charton and Pérez Ruzafa (1998), except that we marked the transect length by extending a tape measure simultaneously to counting fish, and the observer went through the transect only once.

The data (abundance and biomass – total and by species – species richness) were analyzed using hierarchical (nested) analysis of variance (Underwood, 1997). This procedure allows the components of variation to be partitioned among spatial scales, and then the scales that contributed most to the total variation to be identified (Morrisey et al., 1992; Lindegarth et al., 1995). The model for analysing this sampling design is:

$$X_{ijkl} = \mu + L_i + S(L)_{j(i)} + Z(S(L))_{k(j(i))} + T_{ijkl}$$

and the corresponding table of analysis of variance is shown in Table 1.

6.2.2. Results

We observed a total of 52 species (19 families) during this study (Tables 2 and 3). Again, Sparidae (13 spp) and Labridae (11 spp) were the families presenting the highest number of species. Forty of these species were observed at Cabo de Palos, 41 species at Aguilas, and 31 at Isla Grosa. Mean species richness was 14 (± 0.4 SE) species 250 m^{-2} and mean total abundance was 787 (± 59.0 SE) individuals

Table 1

Nested analysis of variance performed on the fish data of the hierarchical sampling design (see text for details), showing the different spatial factors considered (df – degrees of freedom)

Source of variation	Scale (m)	Levels	df	*Fvs*
Locality L	10^4	$l = 3$	2	$S(L)$
Sector $S(L)$	10^3	$s = 3$	6	$Z(S(L))$
Zone $Z(S(L))$	10^2	$z = 3$	18	Residual
Replicate, residual T	10^1	$n = 3$	54	

Table 2
Mean values per transect of the variables describing the fish assemblage structure in the three localities included in the hierarchical sampling design, and total means. Results from the spatial variation study (nested analysis of variance) are shown, indicating the spatial scales at which significant variation exists.

	Cabo de Palos	Isla Grosa	Aguilas	Total	Locality	Sector	Zone
Abundance (individual 250 m^{-2})	951.4	488.74	921.3	787.1	NS	*	*
Biomass (g 250 m^{-2})	109700	10210	28290	49380	NS	*	NS
Species richness (n)	14.2	11.9	17.3	14.5	*	**	*

NS: Non-significant.
* Significant at $P = 0.05$.
** Significant at $P = 0.01$.

250 m^{-2}, while the biomass attained an average of 49 380 ($\pm$16 820.0 SE) g 250 m^{-2}. Seventeen species were observed at only one of the three localities studied: *Serranus atricauda, Trachurus mediterraneus, Coryphaena hippurus, Pomadasys incisus, Sparus aurata, Spondyliosoma cantharus, Symphodus doderleini, Scorpaena porcus*, and *Atherina hepsetus* at Cabo de Palos; *Labrus viridis* at Isla Grosa; and *Epinephelus caninus, Mycteroperca rubra, Parapristipoma octolineatum, Pagellus acarne, Spicara smaris, Scorpaena scrofa*, and *Balistes carolinensis* at Aguilas.

For the total number of individuals, total biomass, mean number of species, and the mean abundance of 34 of the 52 species censused, significant differences were observed ($p < 0.05$) at some of the spatial scales examined (Tables 2 and 3). The three measured assemblage variables, but only seven species among all, showed spatial patchiness at more than one spatial scale. If we consider the significant differences between localities (tens of kilometres apart), the number of species and the abundance of six species showed spatial patchiness at this scale (Tables 2 and 3, Fig. 2). Only one of the 17 species observed at a single locality (*Epinephelus caninus*) showed such a statistical significance of these differences, as a result of the very low abundance and high variability of occurrence of those species. Other 14 species, and all the variables characterizing the fish assemblage (abundance, biomass, and species richness), showed significant differences of their mean abundance between sectors separated thousands of meters (Tables 2 and 3), while 21 species, and the total abundance and the number of species, showed such differences between zones located hundreds of meters apart. The results using species biomass data (instead of abundance) are only

slightly different, thus depicting essentially the same situation.

6.3. Summary

Using two complementary approaches to the study of spatial patterning of fish assemblages in the same geographical area, we have observed how these organisms show a heterogeneous distribution, this heterogeneity existing at various spatial scales, from 10's to 10000's m. At a local scale, mean total number of individuals exhibited a small-scale (180 m) patchy distribution, while mean species richness (S) showed a larger-scale ($\approx$500 m) spatial structure – in this case the analytical technique used (spatial autocorrelation) did not permit us to distinguish between patchiness and gradient. This latest spatial structure was confirmed by the result of a Mantel's test performed between a matrix of geographical distances among quadrats and the matrix of unsigned differences among the values of S in each quadrat. The search for spatial structures along the continuous transect using multivariate data (Mantel's test and Mantel's correlogram) did not detected any pattern, probably reflecting the variety of responses showed by the different species. On the other hand, the nested sampling design showed that this patchiness can exist at other, simultaneous spatial scales: species richness showed significant differences among zones separated by hundreds of m (this scale being coincidental with that showed by autocorrelation analysis), but also among sectors (thousands of meters apart), and even among localities situated tens of kilometers apart. The same can be observed in the case of species composition, mean total abundance, mean total biomass, and for the mean abundance and biomass of most fish

Table 3

Values of mean abundance and mean biomass per transect for the 52 species observed in the hierarchical sampling programme, and mean total values. Results from the spatial variation study (nested analysis of variance) are shown, indicating the spatial scales at which significant variation exists.

	Cabo de Palos		Isla Grosa		Aguilas		Total		Locality	Sector	Zone
	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass			
Engraulis encrasicolus			37.0	50.6	23.8	9.7	20.3	20.1	NS	NS	**
Muraena helena	0.8	1024.6	0.04	24.3	0.2	365.9	0.3	471.6	NS	*	NS
Phycis phycis	0.04	6.6			0.04	1.9	0.02	2.8	NS	NS	NS
Anthias anthias	65.1	189.4			18.7	33.9	28.0	74.4	NS	*	***
Epinephelus costae	0.1	255.7	0.1	47.7	0.1	71.6	0.1	125.0	NS	NS	NS
Epinephelus marginatus	0.2	624.6	0.1	111.8	0.6	801.3	0.3	512.6	NS	*	NS
Epinephelus caninus					0.1	72.2	0.05	24.1	***	NS	NS
Mycteroperca rubra					0.04	100.4	0.01	33.5	NS	NS	NS
Serranus atricauda	0.04	4.4					0.01	1.5	NS	NS	NS
Serranus cabrilla	2.3	75.4	1.5	36.7	1.3	53.8	1.7	55.3	NS	NS	*
Serranus scriba	1.2	45.2	2.3	65.1	3.9	148.9	2.5	86.4	*	NS	*
Apogon imberbis	8.2	39.1	4.1	25.9	68.7	333.3	27.0	132.8	**	NS	**
Seriola dumerilii					2.9	920.8	1.0	307.0	NS	NS	*
Trachurus mediterraneus	0.3	63.5					0.1	21.2	NS	NS	NS
Coryphaena hippurus	0.04	22.5					0.01	7.5	NS	NS	NS
Parapristipoma octolineatum					0.3	16.2	0.1	5.4	NS	*	NS
Pomadasys incisus	0.04	0.6					0.01	0.2	NS	NS	NS
Sciaena umbra	0.9	121.6	0.04	1.0	0.9	82.7	0.6	68.4	*	NS	NS
Mullus surmuletus	0.4	18.3	1.3	39.2	4.3	247.1	2.0	101.7	NS	***	NS
Boops boops	13.1	902.1	20.0	24.6	86.4	244.5	39.8	390.4	NS	NS	*
Dentex dentex	2.9	1.7			0.1	3.0	1.0	0.6	NS	*	*
Diplodus annularis	1.4	36.3	1.4	35.1	5.0	197.6	2.6	89.7	NS	NS	**
Diplodus cervinus	0.3	89.9			0.1	7.8	0.1	32.6	NS	NS	**
Diplodus puntazzo	3.5	543.9	1.4	44.0	3.2	268.0	2.7	285.3	NS	**	NS
Diplodus sargus	9.5	2040.9	2.6	88.2	14.0	1794.5	8.7	1307.9	NS	NS	**
Diplodus vulgaris	25.0	1754.0	14.3	676.5	25.4	1968.2	21.6	1466.3	NS	NS	**
Oblada melanura	33.3	2895.1	4.6	178.2	75.8	5144.4	37.9	2739.2	NS	**	*
Pagellus acarne					1.7	42.1	0.6	14.0	NS	NS	NS
Pagrus pagrus	0.04	23.6	0.04	3.5	1.0	50.1	0.4	25.7	NS	NS	***
Sarpa salpa	37.7	7705.5	4.4	427.2	35.5	3371.3	25.9	3834.7	NS	**	NS
Sparus aurata	0.04	103.9					0.01	34.6	NS	NS	NS
Spondyliosoma cantharus	0.1	26.2					0.05	8.7	NS	NS	***
Spicara flexuosa			6.3	143.5	53.0	2160.7	19.8	768.1	NS	NS	NS
Spicara smaris					1.5	9.9	0.5	3.3	NS	NS	NS
Chromis chromis	527.7	1168.3	308.2	725.6	411.1	890.0	415.7	928.0	NS	**	NS
Coris julis	32.7	103.6	25.9	105.6	39.2	117.9	32.6	109.0	NS	NS	***
Labrus merula	0.04	200.9	0.1	431.9			0.1	210.9	NS	***	NS
Labrus viridis			0.04	4.8			0.01	1.6	NS	NS	NS

Table 3 (*Continued*)

	Cabo de Palos		Isla Grosa		Aguilas		Total		Locality	Sector	Zone
	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass			
Symphodus doderleini	0.04	0.2			0.5	5.7	0.2	2.0	**	NS	NS
Symphodus mediterraneus	0.5	5.4	0.1	1.8	1.1	15.5	0.6	7.5	NS	NS	*
Symphodus melanocercus			0.2	1.6	0.4	3.9	0.2	1.8	NS	NS	NS
Symphodus ocellatus	2.6	6.1	4.7	18.0	7.0	13.7	4.8	12.6	NS	*	NS
Symphodus roissali	0.4	4.1	0.5	6.2	0.6	7.1	0.5	5.8	NS	NS	NS
Symphodus rostratus	0.1	1.4	0.3	2.9	1.1	16.3	0.5	6.9	*	NS	NS
Symphodus tinca	2.6	3409.1	5.8	6453.1	9.0	8462.9	5.8	6108.3	NS	*	*
Thalassoma pavo	99.1	286.7	40.6	103.4	22.0	85.2	53.9	158.5	NS	*	*
Sphyraena sphyraena	40.3	85590.0	0.3	256.1			13.5	28620.0	NS	NS	NS
Mugilidae	0.9	102.5	0.3	74.2	0.7	113.0	0.6	96.6	NS	NS	NS
Scorpaena porcus	0.7	106.8					0.2	35.6	NS	NS	NS
Scorpaena scrofa					0.04	9.2	0.01	3.1	NS	NS	NS
Balistes carolinensis					0.1	27.7	0.02	9.2	NS	NS	***
Atherina hepsetus	37.0	50.6					12.3	16.9	NS	NS	***

NS: Non-significant.
* Significant at $P < 0.05$.
** Significant at $P < 0.01$.
*** Significant at $P < 0.001$.

species observed throughout the study. The spatial structure detected by the different analytical techniques are different depending of the variable and the species.

A variety of factors can be called on to explain this observed patchiness, as developed in the above paragraphs. We could categorized them into physical or abiotic factors (e.g., habitat structure), biotic factors, and disturbances, both natural (e.g., Renaud et al., 1996) or man-caused (e.g., Davis and Tisdell, 1995; Auster, 1998). Using a multiscaled approach such as that presented here, in combination with the measure of environmental variables, it is possible to build a catalogue of causal hypotheses to account for the observed pattern (García Charton et al., in press). As argued throughout this article, natural populations and assemblages experience a great variety of environmental pressures, each of which are acting on different levels of organization, through different mechanisms, and at different (and often simultaneous) spatial and temporal scales, and given as a result an heterogeneous pattern in space and time. Only by taking this multiscaled patchiness into account we can avoid the problem of confounding. Also, when studying the change over time of the fish assemblage, it is still possible to confound temporal variability with small-scale spatial variation, which thus must be characterized with precision. Furthermore, as noted by Morrisey et al. (1992), 'the spatial patterns detected (. . .) are likely to change with time', so that the need to replicate studies such as those described here in different sites and at different moments becomes evident.

7. Conclusions: consequences for monitoring and evaluation of marine reserves

The hierarchical patchiness of habitats imposes constraints when undertaking the study of the ecological effects of protection in marine areas. As a first, obvious (but not trivial) consequence, it is the consideration that our capability to detect and explain the effects of protection depends mainly on the choice of adequate spatial (and temporal) scales of study. The scale of study has to be elucidated using non-arbitrary, operational methods (Wiens, 1989), keeping in mind that scale is dependent on the species and the pro-

cesses under research. Selecting a priori the scale of study could invalidate the conclusions due to anthropogenic biases of perception.

A second consequence of the seascape approach is that, at a given scale, habitat structure has to be measured to control the interference between ''reserve effect'' and ''habitat effect''. A first source of confounding emerges from the fact that usually we establish marine reserves in zones that present structurally complex habitats (rocky boulders, caves, seagrass meadows), and consequently already support a rich and diverse fauna (what would happen if we protected 'barren' or structurally simpler marine areas?). In some cases, naturally complex, but non-protected marine areas, present even more diverse ichtyofauna than neighbour protected areas, which present simpler habitats (García Charton et al., unpublished data), so that the reserve effect can be masked by that of habitat structure. The measure of habitat features when evaluating the effect of protection has been performed on only a few occasions (e.g., Roberts and Polunin, 1992; Polunin and Roberts, 1993; Jennings et al., 1996b). In some other cases the habitat structure has been grossly estimated visually before performing censuses (e.g., Bell, 1983; García Rubies and Zabala, 1990; Harmelin et al., 1995). Structural habitat has to be of primary concern when designing field experiments aiming to measure the reserve effect.

A third corollary emerging from the above discussion is that monitoring studies for marine reserves have to be undertaken considering spatio-temporal heterogeneity. In this sense, processes involved in the ''reserve effect'' must be considered as an environmental (positive) impact, and, consequently, all the discussion about impact assessment studies (Schmitt and Osenberg, 1996; Underwood, 1997) applies to the topic of marine reserves (Jones et al., 1992). Ideally, multiple protected areas should be compared with the same number of control (non-protected) areas, before and after the protection, and considering multiple nested spatial and temporal scales (A.J. Underwood, personal communication). The duration of this kind of study has to be long enough to be able to differentiate between short-term variability and long-term trends (see Menge, 1997).

Finally, as a general statement, the multiscale, hierarchical structure of seascape should be adopted as an integrating principle when designing a research

programme aiming to understand the effect of protection from fisheries. Several authors have already considered some aspect of spatial and temporal heterogeneity when studying the reserve effect (e.g., Man et al., 1995; García Charton et al., unpublished data). We argue that seascape perspective has to be developed (definition of problems and objectives, design of monitoring and sampling programmes, elucidation of relevant spatial and temporal scales for the appropriate acquisition and analysis of data, building up of models and theory, etc.), and could serve as a way of integrating the diversity and complexity of the responses of communities to the effects of protection in marine reserves, allowing a better management of this important tool.

Acknowledgements

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