

Matching spatial distributions of the sea star *Echinaster sepositus* and crustose coralline algae in shallow rocky Mediterranean communities

Adriana Villamor · Mikel A. Becerro

Received: 20 November 2009 / Accepted: 31 May 2010 / Published online: 11 June 2010
© Springer-Verlag 2010

Abstract Understanding why a species is present in a particular location and the consequences of its presence is complex but necessary to identify the mechanisms that generate and maintain ecological diversity. The common sea star *Echinaster sepositus* can be either very abundant or non-existing in nearby localities of the western Mediterranean. Yet, the factors that shape its distribution and the impact of the sea star on natural communities remain uninvestigated. Here, we quantified multiple biotic and abiotic factors that may affect the distribution of *E. sepositus* and tested whether this sea star can shape the organization of the community it inhabits. Our results showed that the distribution of this sea star was highly contagious and positively correlated with the abundance and distribution of crustose coralline algae from tens of meters to tens of kilometers. Despite significant differences in community composition between localities with high or low abundance of the sea star, experimental addition of *E. sepositus* to natural communities failed to shift the composition of the algal community in 4 months. Overall, our results suggest that within habitat variability in the abundance of crustose coralline algae may explain the abundance of *E. sepositus* at multiple geographic scales, emphasizing the need to investigate small-scale processes at larger geographic scales.

Introduction

The study of the mechanisms that determine the presence and abundance of local species is basic to understand species diversity and the organization and functioning of natural communities. The complexity of the multiple factors acting at varying temporal and spatial scales makes predicting whether a species is present in a particular location very challenging. On a local scale, species composition may be determined by a few environmental variables that filter a larger pool of species. According to this niche assembly view, physiological processes and biotic interactions play a major role in community composition (Tilman 1985; Keddy 1992; Grace 1999). Stochastic events at large temporal and spatial scales, local extinction, and long distance dispersal are also known to explain species diversity (Tilman 1994; Eriksson 1996; Hubbell et al. 2001).

Habitat variability correlates with species diversity and depends on the spatial scale investigated (Davidowitz and Rosenzweig 1998). Large-scale surveys comprise multiple variability sources including but not restricted to geographic and habitat variability (e.g., Fabricius and De'ath 2001). At the opposite end, small-scale studies look for the most homogeneous habitats in order to discover the smallest variability (Benedetti-Cecchi and Cinelli 1995). These small-scale variability studies have received little attention, but they seem to play a major role in determining and maintaining diversity (Izsak and Price 2001; Hewitt et al. 2005). In fact, the importance of small-scale habitat variability could be underestimated because small-scale habitat variability can result in large-scale variability patterns if the habitat itself changes across larger scales (Helmuth et al. 2006; Rilov and Schiel 2006; Chapman and Underwood 2008).

Communicated by P. Kraufvelin.

A. Villamor (✉) · M. A. Becerro
Center for Advanced Studies of Blanes (CEAB, CSIC),
Acc Cala S Francesc 14, 17300 Blanes (Girona), Spain
e-mail: villamor@ceab.csic.es

Sea stars are marine animals that inhabit virtually every ecosystem regardless of latitude and depth (Hyman 1955). Sea stars also are voracious feeders that can alter communities by preferential predation (Menge 1982; Duggins 1983; Himmelman and Dutil 1991). Despite the abundance of information on the role of sea stars as major drivers of community organization and functioning, there is no available information on the role of sea stars in benthic Mediterranean communities. *Echinaster sepositus* (Retzius 1783) is one of the most common and abundant sea stars in the Mediterranean Sea, yet information on the biology of this sea star is fragmentary and contradictory. This is particularly obtrusive for its feeding habits (Vasserot 1961; Ferguson 1969), which are based on casual observations, and accurate information is lacking. Biological information on other species of the genus *Echinaster* or the family Echinasteridae has been equally overlooked. Ecologically, the distribution of *E. sepositus* varies as a function of cover of sand, algae, and depth (Entrambasaguas et al. 2008), although the exact nature of these relationships is complex and irresolute. The abundance of *E. sepositus* can also vary tremendously between nearby localities that have no conspicuous differences in community composition, suggesting that the abundance of this species could be affected by biotic or abiotic factors acting at scales of hundred of meters or less (Underwood and Chapman 1996; Chapman and Underwood 2008). In short, the causes and consequences behind the variable abundance of *E. sepositus* in Mediterranean shallow rocky communities remain open questions.

The goal of our study is twofold as we aimed at increasing our understanding of (1) the factors that can regulate the spatial distribution of *Echinaster sepositus* and (2) the consequences that the sea star may have in Mediterranean shallow rocky communities. To do so, we quantified the abundance of *E. sepositus* and several biotic and abiotic variables within shallow algal-dominated communities. Shallow communities above 11 m of depth are characterized by homogeneous spatial patterns when compared to communities below that depth (Garrabou et al. 2002). Rather than investigating a particular location extensively, we targeted the variability within this community type from multiple locations spread over 150 km of coastline. Thus, our approach aimed at a level of variability usually associated with small-scale studies but over a larger geographic scale. This particular approach allowed us (1) to quantitatively characterize the community that *E. sepositus* inhabits, (2) to establish the degree of variability in abiotic factors and community composition between locations with high and low sea star abundance, (3) to look for correlates of sea star abundance, and (4) to describe patterns of spatial distribution of the sea star and correlates from a scale of tens of meters to tens of kilometers. This first observational part of our study was designed to look for potential causes

behind the variation in abundance of *E. sepositus* and to generate testable hypotheses well supported by field data in our study area. Then, in the second part of our study, we experimentally tested whether *E. sepositus* had the capacity to induce the differences we observed between locations with low and high abundance of the sea star. This approach is particularly relevant to assess the causes and consequences of the large variation in the abundance of *E. sepositus* in these types of communities.

Materials and methods

Organism and area of study

Echinaster sepositus (Echinodermata, Class Asteroidea, Order Spinulosa, Family Echinasteridae) is distributed along the eastern Atlantic and the Mediterranean Sea (Riedl 1983; Ocaña Martín et al. 2000). This sea star is easily recognized by a small disk with five slender cylindrical rays from bright orange to blood red, a reticulated skeleton with open meshes, and single or few spines at the nodes. Its only known predator is the gastropod *Charonia lampas lampas* (Linnaeus 1758), distributed along the western Mediterranean and eastern Atlantic but virtually extinguished in our study area due to overfishing (Mas Cornet 2005). No information is available about predation at earlier stages of development. As a consumer, *E. sepositus* is traditionally considered a sponge feeder (Vasserot 1961; Sarà and Vacelet 1973) even though it causes negligible damage and mortality to sponges (Ferguson 1969; Maldonado and Uriz 1998). Also, *E. sepositus* has been found in feeding position on a variety of substrates including multiple invertebrates, algae, and sediment (Ferguson 1969).

Our study took place on shallow rocky bottoms off the Costa Brava, Spain (northwestern Mediterranean Sea), at a depth between 5 and 10 m. Mediterranean shallow communities are well characterized by the dominance of photophilic algae. At the depth range of our study, the community is formed by the characteristic algal and invertebrate species found on moderately calm conditions that demarcate a homogeneous facies (Pérès and Picard 1964; Ros et al. 1985; Garrabou et al. 1998). Above 5 m, there is a shift toward species more prone to strong water movement resulting in a distinct community where *Echinaster sepositus* is incidental. Below ten meters, the incidence of sciaphilous species becomes noticeable changing the overall perception of the landscape. Although *E. sepositus* may be abundant below 10 m, we restricted our sampling to the 5–10 m depth range because of the large variation in sea star densities at those depths and the consistency of the landscape in our study area. This restriction also avoided the complex relationship between this sea star and depth

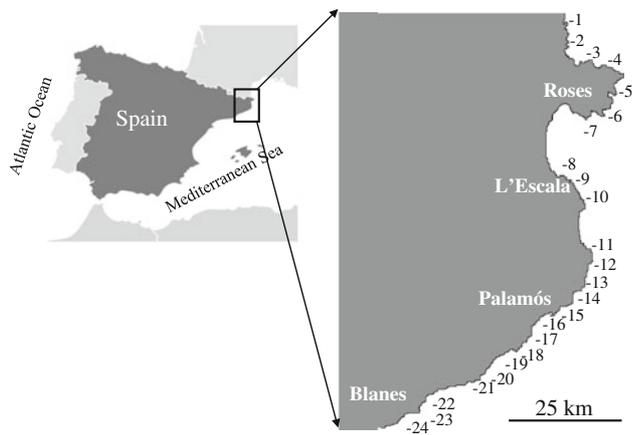


Fig. 1 Situation map of the study area in the northwestern Mediterranean. Numbers indicate the 24 localities surveyed. From north to south: Port Bou, Colera, Faro de S'Arnella, Port de la Selva, Cala Culip, Port lligat, Cala Montjoi, Cala Mateua, Montgri, Medas, Ses Negres, Aiguafreda, Tamariu, Llafranc, La Fosca, Palamós, S'Agaro, Port Salvi, Salionç, Tossa, Muladera, Cala St Francesc, Niell St Francesc, and Pta. Sta Anna

noticed by other authors (Entrambasaguas et al. 2008). We haphazardly selected 24 locations covering 150 km of coast (Fig. 1). Three gap areas in our design resulted from complex access (in the southernmost gap) and absence of rocky bottoms (in the remaining two gaps). Our study sites included two submarine mountains, 11 bays, seven sites subject to intense boat traffic in summer time, and four sites with limited access for people and boats. Six of these sites are inside marine protected areas (Cape Creus, Medes Islands, and Ses Negres).

Sampling of biotic and abiotic variables

From June to August 2006, we SCUBA dove in all 24 locations and quantified the abundance of fish, algae and sessile invertebrates, echinoderms, and a number of abiotic variables. These variables quantify the sessile community, the major consumers in the system (Hereu 2006; Hereu et al. 2008), and important environmental factors that shape their distribution (Ros et al. 1985; Garrabou et al. 1998; Virgilio et al. 2006).

In each location, we haphazardly placed a 50-m transect line between 5 and 10 m depth. We used underwater visual census (UVC) in a 2-m-wide strip at each side of the transect line to quantify fish abundance. Specifically, we recorded the number of fish specimens belonging to the most common and abundant demersal fish families in the study area (Labridae, Sparidae, and Serranidae). *Sarpa salpa* (Linnaeus 1758) was treated independently of the family Sparidae to which it belongs to account for functional differences in their feeding behavior. *S. salpa* is a strict herbivore with a strong aggregating behavior as

opposed to the remaining sparid species which are carnivores or omnivores.

In the same transect line, we quantified the sessile composition by recording every 50 cm the organism present underneath the line (point-intercept method, 100 points total). Crustose coralline algae (also referred to as encrusting red algae, corallines or crusts, following Steneck et al. 1991) such as *Lithophyllum sp.*, *Mesophyllum sp.*, and *Peyssonnelia sp.* were recorded when not overgrown by other algal species (Tuya and Haroun 2006). We combined algal species into functional groups because they represent ecologically distinct and relevant groups suitable to examine overall changes in benthic community (Britton-Simmons 2006; Perner and Voigt 2007). We adapted for our study the algal functional groups described by Steneck and Watling (1982) (Table 1), which are widely used and strongly correspond to specific ecological characteristics (Littler and Littler 1984). Species of sessile invertebrates were also classified according to their zoological group as sponges, bryozoans, ascidians, hydrozoans, anthozoans, and cirripeds. We also quantified the number of sea urchins and number of the sea stars *Echinaster sepositus* and *Marthasterias glacialis* (Linnaeus 1758) along a 50-m²-wide strip, centered in the transect line. The most abundant sea urchin species in the area was *Paracentrotus lividus* (Lamarck 1816). A few specimens of the sea urchin *Arbacia lixula* (Linnaeus 1758) were noticed in some transects, although numbers were low as this species inhabits preferentially artificial breakwaters (Palacin et al. 1998b). To facilitate underwater quantification, we included both species in our sea urchin category as main invertebrate grazers on these communities.

All abiotic variables were measured in the same transect line used to quantify biotic data. We used the chain-and-tape method to calculate substrate rugosity (Risk 1972). Every five meter along the transect line, we recorded depth (dive computer), slope (as the arcsin of the depth difference between the transect line and one meter down the slope), and orientation (compass). The ten individual measurements of depth, slope, and orientation for each transect were averaged to a single value for each location. Satellite temperature data for each of the 24 locations during the sampling months were extracted from <http://oceancolor.gsfc.nasa.gov>.

Rather than extensively sampling a single or a small group of locations based on specific characteristics, we sampled 24 locations over 150 km of coastline to assess the variability of the target algal-dominated community. We conceived this observational part of our study as an exploratory analysis to assess whether the abundance of *Echinaster sepositus* correlated with other biotic and abiotic variables in the community, which could provide testable hypotheses on the causes of sea star variation. We relied on

Table 1 Functional groups used to classify algal species, main anatomic traits of the group, and examples found in our study area (Modified from Steneck and Dethier 1994)

Functional group	Comparative anatomy	Examples
Filamentous	Uniseriate line of equal cells	<i>Cladophora</i> sp., <i>Falkenbergia rufolanosa</i>
Foliose	Differentiated cortex with one layer cells medulla	<i>Codium bursa</i> , <i>Dictyota dichotoma</i> , <i>Flabellia petiolata</i>
Corticated	Differentiated cortex with multilayered medulla	<i>Gelidium latifolium</i> , <i>Halopteris scoparia</i> , <i>Sphaerococcus coronopifolius</i>
Calcareous articulated	Multilayered with calcified cortex	<i>Amphiroa rigida</i> , <i>Corallina elongata</i> , <i>Halimeda tuna</i> <i>Acetabularia acetabulum</i> ^a
Crustose coralline	Cortex and medulla both calcified	<i>Peyssonnelia squamaria</i> , <i>Mesophyllum lichenoides</i> , <i>Lithophyllum incrustans</i>

^a Unicellular species. Included in the group “Calcareous articulated algae” because of its size and heavy calcification

a regression style approach as opposed to an analysis of variance (ANOVA) approach, since all our variables were continuous and we lacked quantitative information on sea star variability as to define ecological relevant categories (Gotelli and Ellison 2004). Accordingly, each location in our study represented a replicate of the community, so there was no need for additional replication within locations. Our data, however, were representative of the location and accounted for the small-scale variability within each particular location. Our 50-m-long UVCs provided ample representation of rocky fish assemblages in the Mediterranean, where 25-m-long UVCs are often used (Harmelin-Vivien et al. 2008). As to the benthic community, our 50-m-long transect lines spanned the range of spatial variability present in each location due to differences in orientation, presence of high densities of herbivores, species patchiness, or other small-scale sources of variation. As an example, 50 and 80% of the species we found occurred within the first 10 and 25 m, respectively (data not shown). Thus, the spatial grain of our 50-m-long transects was above the usual size of sample unit in these types of studies and complements the regional spatial extent of our study.

Analyses of field data

We used linear regression to test for independence between abiotic variables. We then tested whether the abiotic variables were affecting biotic composition with the BIO-ENV procedure of Primer 6 (Clarke and Warwick 2001). This procedure calculates a Bray–Curtis similarity matrix (on square-root transformed abundance of the biotic variables) that is compared to multiple combinations of the abiotic variables at steadily increasing levels of complexity, until the best match of biotic and environmental patterns is found (or lack thereof). Since the BIO-ENV procedure evaluates relationships at a community level, we used multiple correlation analysis (Systat, SPSS 1999) to specifically test

whether the abundance of *Echinaster sepositus* was correlated with any abiotic variables.

We classified the 24 sampling sites as a function of the abundance of *Echinaster sepositus*. High and low density locations referred to sites with above and below average sea star density for the whole study area. We then used analysis of similarity (ANOSIM) to test whether community organization varied between these two groups with contrasting sea star abundance. An exploratory similarity breakdown using the SIMPER procedure available in the PRIMER software assigned the relative contribution of the biotic variables to the dissimilarities between locations with high and low abundance of *E. sepositus* (Clarke and Ainsworth 1993). Based on these results, we then used multiple correlation analysis (Systat, SPSS 1999) to test for the relationship between the abundance of the sea star and every variable that contributed to the 50% dissimilarity between high and low abundance locations.

For those species whose abundances correlated with *Echinaster sepositus*, we used the χ^2 test of the variance to mean ratio as an index of dispersion (IOD) to check whether they matched their spatial distributions (Elliot 1977). We used abundance data from each location and pooled data from multiple groups of neighbor locations to calculate the IOD at increasing geographic scales from tens of meters to tens of kilometers. The smallest scale corresponded with our 50-m transects in each of the 24 locations. We then pooled abundance data from 2, 3, 4, 6, 8, and 12 neighbor locations (12 was the maximum number of locations that we could pool and still had two independent groups as replicates). These groups of neighbor locations corresponded with distances of 6, 13, 18, 31, 42, and 68 km, respectively (average of the distance between the most distant locations in each group). We then tested whether the spatial distributions of *E. sepositus* and other selected species or groups were correlated.

Experimental manipulation of sea star abundance

To test the hypothesis that *Echinaster sepositus* can alter community organization, we manipulated sea star densities in a shallow rocky area known as Punta Santa Anna. We selected this particular location because of the presence of several rock patches located in a sandy shallow area right next to our location 24. Natural densities in this location were below the average found in the whole study area, but *E. sepositus* was actually absent on these particular rocks. We targeted this type of landscape so individual rocks could be used as independent treatments isolated by sandy bottoms, which acted as a natural barrier to prevent sea star dispersion to adjacent areas. We also selected for rocks that were appropriate to design a manageable experiment, i.e., large enough to incorporate several sea stars, small enough to prevent a massive sea star rearrangement, and with comparable conditions. We found nine rocks off the coastal rocky bottom at a depth of eight meters. The low number of appropriate replicates and the lack of knowledge on the actual effect of sea star density on community organization suggested against a traditional “ANOVA-like” experiment. Rather than categorizing sea star density to test for a few arbitrary values with low levels of replication, we chose an experimental regression approach and used regression to fit our data. Experimental regression is a very efficient and ideal design to characterize changes in community composition with increasing sea star densities (Gotelli and Ellison 2004).

We selected for nine density levels that included natural densities and beyond the maximum density of 0.4 specimens/m² found in our region (0, 0.05, 0.1, 0.2, 0.4, 0.6, 0.8, 1.1, and 1.4 specimens/m²). We then used analysis of covariance (ANCOVA) to test for the effect of density and time (beginning and end of the experiment) on the percent cover of sessile organisms. A statistically significant “density × time” interaction term would indicate that sea stars have an effect on community organization (effect of density varies as a function of time). The experiment lasted 4 months (November 2006 to February 2007), and sea star densities were monitored weekly to ensure constant density values throughout the experiment.

For each rock, we quantified the sessile composition by recording the organism present underneath randomly generated points. The number of points varied proportionally to rock area to prevent bias in our sampling effort as a function of rock size. Specifically, we sampled 100 points every 50 m² of rock, ranging between 60 and 120 points for our smallest 30 m² and largest 60 m² rocks. Prior to the ANCOVA, we used factor analysis (FA) to reduce the number of species to a few coherent groups (factors) of species that were correlated with one another within groups but

largely independent between groups (Tabachnick and Fidell 2001). These groups can reduce notably the number of variables with little loss of information (Tabachnick and Fidell 2001). Specifically, we used a principal component analysis extraction (PCA) with varimax rotation and a minimum eigenvalue of 1 to estimate the number of factors. The resulting independent factors were used as variables in a multivariate analysis of covariance (MANCOVA) to test whether community composition varied as a function of sea star density and time. Evaluation of assumptions of normality, homoscedasticity, linearity, multicollinearity, and homogeneity of slopes was satisfactory (Tabachnick and Fidell 2001).

Results

Correlates of sea star abundance

Except temperature ($R = 0.830$, $P < 0.001$), none of the abiotic variables quantified were associated with geographic position. We identified 49 sessile benthic species although turf, *Mesophyllum* sp, *Halopteris* sp, and *Dilophus* sp occupied over 50% of the total area (Fig. 2).

Family fish abundance varied between locations (Table 2). Labrids and sparids were the most abundant fish groups. Serranids were never abundant in the study area, while *Sarpa salpa* was locally very abundant (Table 2).

Sea urchins were the most abundant vagile organisms in the benthos and *Echinaster sepositus* the most abundant sea star. The average abundance of *E. sepositus* for the whole study area was 4.29 ± 1.07 (mean \pm SE, Table 2) and showed a significant geographic trend, being more abundant in northern than southern locations (Fig. 3; $\chi^2 = 19.660$, $df = 1$, $P < 0.001$). We found no *E. sepositus* in nine out of the 24 locations (Fig. 3) and a single individual of *Marthasterias glacialis* in each of six locations (Table 2).

All the quantitative environmental variables (temperature, rugosity, depth, orientation, and substrate slope) were unrelated to each other (correlation analysis, $P > 0.05$ for all comparisons). At the community level, abiotic factors failed to explain community organization on our study area as evaluated by the Primer’s BIO-ENV procedure ($R = 0.136$, $P = 0.500$). Abundance of *Echinaster sepositus* was only correlated with substrate slope ($R = 0.414$, $P = 0.045$) before, but not after, Bonferroni correction.

Community composition varied significantly between locations with high (>5 individuals) and low (≤ 5 individuals) abundance of *Echinaster sepositus* (ANOSIM, Global $R = 0.267$, $P = 0.017$). Sea urchins, the herbivore fish *Sarpa salpa*, crustose coralline algae, sparid fishes, and calcareous articulated algae were responsible for 50% of the dissimilarity

Fig. 2 Cumulative abundance (%) of the algae and sessile invertebrates quantified in the 24 locations surveyed. Dotted line indicates 50% of cumulative abundance

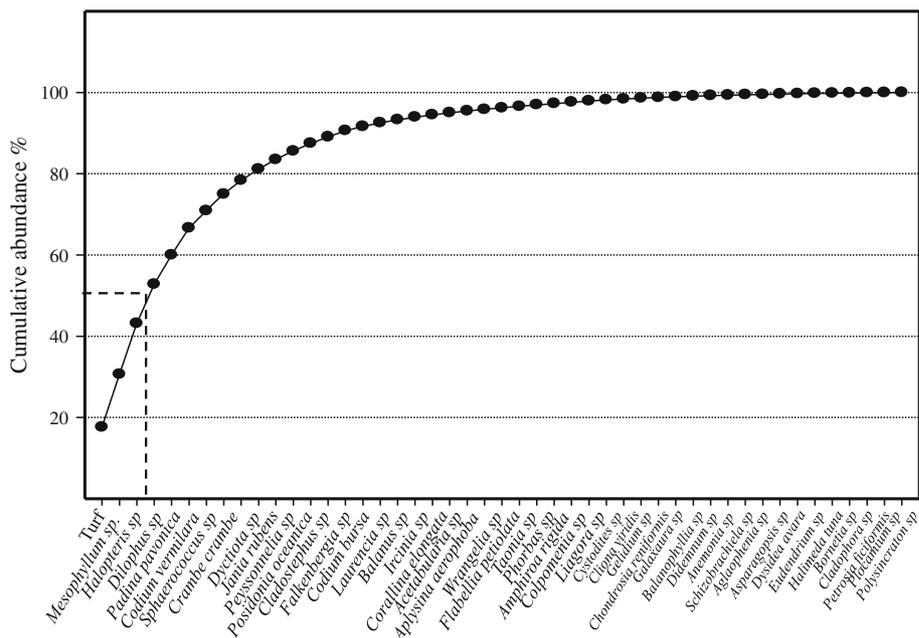


Table 2 Minimum, maximum, and mean ± standard error values of fishes and echinoderms in the studied area

Organism	Min	Max	Mean ± SE
Labridae	13	66	32 ± 3.32
Sparidae	2	66	23.17 ± 3.25
Serranidae	0	12	5.08 ± 0.85
<i>Sarpa salpa</i>	0	55	8.66 ± 3.24
Sea urchins	22	259	108.75 ± 14.85
<i>Echinaster sepositus</i>	0	20	4.29 ± 1.07
<i>Marthasterias glacialis</i>	0	1	0.25 ± 0.09

Fish data are number of individuals found in a 50 m × 4 m strip. Echinoderm data are number of individuals in a 50 m × 1 m strip

between sites with high and low abundance of the sea star (SIMPER analysis, Table 3). Sea urchins and calcareous articulated algae were more abundant in locations with low abundance of *E. sepositus*, while *S. salpa*, sparid fishes, and crustose coralline algae were more abundant in locations with high abundance of the sea star (Table 3).

Sea star abundance was positively correlated with the abundance of crustose coralline algae, even after Bonferroni correction ($R = 0.662$, $P < 0.001$). As *Echinaster sepositus*, this algal group was more abundant in northern than southern locations ($\chi^2 = 22.688$, $df = 1$, $P < 0.001$). The spatial distribution of *E. sepositus* and crustose coralline algae were strongly correlated as shown by the χ^2 test of their index of dispersion ($R = 0.982$, $P < 0.001$, Fig. 4), which also showed a trend from contagious to random distributions from local to regional scales (Fig. 4).

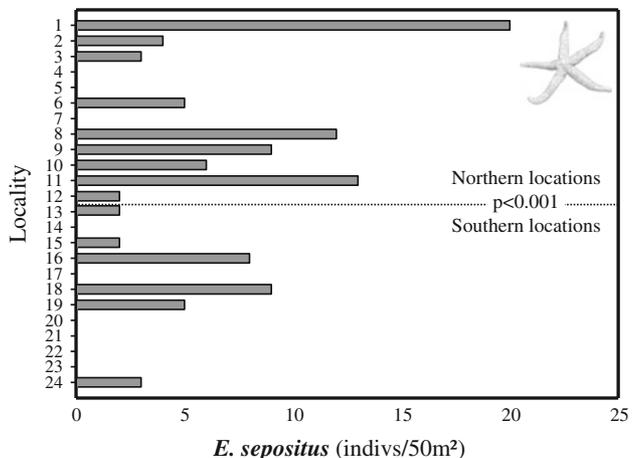


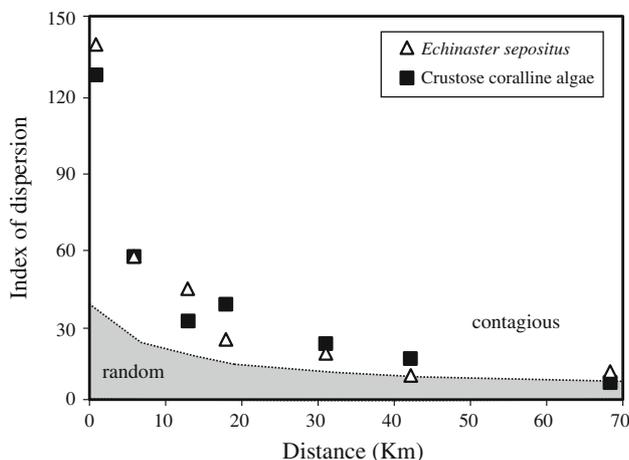
Fig. 3 Bar diagram of the number of *Echinaster sepositus* in 50 m² for each location. Locations ordered from north (top) to south (bottom). Significant differences in sea star abundance between northern and southern locations (dotted line) tested by contingency table analysis ($\chi^2 = 19.660$, $df = 1$, $P < 0.001$)

Effects of sea stars on community organization

We quantified a total of 37 sessile species on the experimental rocks. Algae dominated in number of species and percent cover (algae: 22 species, 88.8% cover; sponges: 9, 9.4%; cnidarians: 4, 0.9%, and ascidians: 2, 0.9%). Factor analysis of the 38 species (including bare rock) resulted in 11 independent factors that explained 90.08% of the total variance (Table 4). Multiple analysis of covariance (MANCOVA) on the 11 factors showed no significant “density × time” (Wilk’s $\Lambda = 0.327$, $F = 0.750$, $P = 0.682$),

Table 3 Functional groups and species average abundance, on square-root transformed data, and their contribution to dissimilarity (%) between localities with high and low density of *Echinaster sepositus*

Variables	Aver. Abund. Low dens. sites	Aver. Abund. High dens. sites	% Dissim.
Sea urchins	10.32	8.64	15.69
<i>Sarpa salpa</i>	1.69	2.49	10.37
Crustose coralline algae	3.10	5.16	8.76
Sparids	4.42	4.76	7.98
Calcareous algae	1.88	1.35	7.00
Corticated algae	4.74	3.74	6.07
Filamentous algae	4.50	3.58	6.01
Serranids	2.18	1.41	5.66
Labrids	5.59	5.28	5.66
Sponges	2.44	1.74	5.64
Foliose algae	5.23	5.49	4.37
<i>Posidonia oceanica</i>	0.92	0.14	3.92
Free space	0.59	0.49	3.00
Others	7.13	8.99	9.87

**Fig. 4** Index of dispersion as calculated by the χ^2 test of the variance to mean ratio of *Echinaster sepositus* (open triangle) and crustose coralline algae (solid square) as a function of increasing population distance. Both species showed a highly contagious spatial distribution (white area) at a scale of tens of meters that shifted toward randomness (gray area) with increasing distance ($R = 0.982$, $P < 0.001$)

no “density” effect (Wilk’s $\Lambda = 0.217$, $F = 1.641$, $P = 0.305$), but a significant “time” effect (Wilk’s $\Lambda = 0.002$, $F = 245.305$, $P < 0.001$) that is exclusively driven by factor 1 (ANOVA, $F = 33.328$, $P < 0.001$). This factor comprises seasonal species of algae and invertebrates very common in this area and whose abundances might dramatically change in such time period (Table 4).

A specific ANCOVA on the percent cover of crustose coralline algae as a function of time and density showed

Table 4 Factor analysis (FA) on the percent cover of the 38 sessile species (including bare rock) quantified in the community where densities of *Echinaster sepositus* were manipulated

Species	Factor	Coefficient	Variance explained (%)
<i>Dyctiota</i> sp	A 1	−0.854	15.16
<i>Cladophora</i> sp	A 1	0.799	
<i>Falkenbergia</i> sp	A 1	0.776	
<i>Dilophus</i> sp	A 1	0.746	
<i>Aglaophenia</i> sp	C 1	−0.684	
<i>Clavellina</i> sp	T 1	−0.645	
<i>Codium vermilara</i>	A 1	0.615	
<i>Plocamium</i> sp	A 1	−0.538	
<i>Halocynthia papillosa</i>	T 2	−0.965	9.61
<i>Cereus pedunculatus</i>	C 2	−0.916	
<i>Jania Rubens</i>	A 2	−0.746	
<i>Corallina elongata</i>	A 2	−0.665	
<i>Ircinia</i> sp	S 3	−0.825	8.45
<i>Codium bursa</i>	A 3	−0.774	
Turf	A 3	0.654	
<i>Chondrosia reniformis</i>	S 3	−0.616	
Bare rock	– 4	−0.986	8.41
<i>Scopalina</i> sp	S 4	−0.986	
<i>Mesophyllum</i> sp	A 4	−0.639	
<i>Peyssonnelia</i> sp	A 4	−0.559	
<i>Balanophyllia</i> sp	C 5	−0.955	9.06
<i>Amphiroa</i> sp	A 5	−0.955	
<i>Padina pavonica</i>	A 5	−0.591	
<i>Sphaerococcus</i> sp	A 5	0.567	
<i>Cladostephus hirsutus</i>	A 5	−0.544	
<i>Aglaozonia</i> sp	A 6	−0.929	8.67
<i>Halopteris</i> sp	A 6	−0.717	
<i>Phorbas fictitius</i>	S 6	−0.653	
<i>Halimeda tuna</i>	A 6	−0.509	
<i>Petrosia</i> sp	S 7	−0.904	7.19
<i>Rhodymenia</i> sp	A 7	−0.594	
<i>Phorbas tenacior</i>	S 7	−0.582	
<i>Dysidea avara</i>	S 8	−0.905	8.08
<i>Flabellia petiolata</i>	A 8	−0.664	
<i>Crambe crambe</i>	S 8	−0.504	
<i>Gelidium latifolium</i>	A 9	−0.915	5.09
<i>Corticium candelabrum</i>	S 10	−0.833	5.18
<i>Eunicella singularis</i>	C 11	−0.944	5.18

To facilitate interpretation, only coefficients with absolute value larger than 0.5 are shown. Capital letters in the first column indicate algae (A), cnidarians (C), sponges (S), and tunicates (T). The resulting independent factors after FA explained 90% of the total variance

that none of the factors neither their interaction was significant (density: $F = 1.438$, $P = 0.249$; time: $F = 0.888$, $P = 0.361$; density \times time: $F = 0.016$, $P = 0.902$).

Discussion

It is widely accepted that habitat variability provides more opportunities for species to find and occupy their niche, regulating many ecological processes including the abundance and distribution of species (Zajac et al. 2003; Hewitt et al. 2005). In our study, we targeted a specific, representative, and well-established algal community in the western Mediterranean seeking for a reasonably homogeneous environment where to investigate the abundance of the sea star *Echinaster sepositus* over a larger regional scale of 150 km. In this sense, our study assessed whether small variation within homogeneous habitats can explain differences in species abundance at larger geographic scales, combining goals associated with small- and larger-scale studies (Benedetti-Cecchi and Cinelli 1995; Ruitton et al. 2000; Fabricius and De'ath 2001). Our study showed significant differences between nearby communities with high and low abundance of *E. sepositus*. Although several species contributed to such differences, we found that only percent cover of crustose coralline algae was correlated with abundance of sea stars. Moreover, the indexes of dispersion of these species from tens of meters to tens of kilometers were highly correlated, supporting the matching spatial distributions of these species in our study area. Multiple biological and statistical arguments could be behind the rationale of this relationship. Our results could either stem from a spurious statistical relationship between crustose coralline algae and sea star abundance, be the result of a direct relationship between them, or be caused by a third unidentified variable.

Although a spurious correlation between the abundance of *Echinaster sepositus* and crustose coralline algae cannot be completely ruled out, statistical and biological evidence suggests otherwise. Because we considered over 40 biotic and abiotic variables in our study, the possibility to obtain some meaningless but statistically significant correlations between them looms large. However, we believe this is unlikely in our study because of statistical and biological reasons. Rather than “data snooping” with our whole data set (Westfall and Young 1993), we searched for correlates of sea star abundance in five abiotic and five biotic variables that were selected based on the results from broader analysis at a community level. This rationale is similar to the bioassay-guided fractionation used for example in chemical ecology to identify the specific compound(s) responsible for an ecological role (Becerro et al. 2001), although our study does test the same data multiple times. To decrease the probability to reject a true null hypothesis (Type I error), we used Bonferroni adjustment to correct our correlations. In our study, only the percent cover of crustose coralline algae was significantly correlated with sea star abundance after Bonferroni correction. Statistically, the probability to obtain by chance such a significant

correlation in a series of 10 tests (as calculated by the Bernoulli equation) is in fact below the traditional 0.05 significant level ($P = 0.010$, Moran 2003). Beyond the relationship between the species abundances, we also found a highly significant correlation between the patterns of distribution of both species, as indicated by their IOD. A number of ecological mechanisms make more plausible arguments for this relationship.

Here, we set forth the hypothesis that the abundance of *Echinaster sepositus* may be mediated by crustose coralline algae. This hypothesis is based on the lack of relationship between sea star abundance and abiotic factors, the high correlation between the abundance and spatial distribution of crustose coralline algae and *E. sepositus*, and the incapacity of the sea star to induce shifts in community organization during the course of our experiment.

We found no relationship between abiotic variables and community composition. This is likely a consequence of the narrow range of environmental variability covered in our study. Shallow Mediterranean rocky communities are dominated by algae, whose composition is known to vary as a function of depth (Boudouresque 1985; Gili and Ros 1985). Orientation, rugosity, and slope are also known to regulate the distribution of sessile organisms (Diez et al. 2003; Tuya and Haroun 2006; Roberts et al. 2006). The 24 locations we investigated in our study targeted a specific algal community dominated by species of moderately calm conditions that demarcated a homogeneous facies (Pérès and Picard 1964; Ros et al. 1985). The abundance of *Echinaster sepositus* in particular was also unrelated to the abiotic variables investigated in our study, except for a weak correlation with slope that failed to pass Bonferroni correction. Sand, algal cover, and depth correlate with the abundance of *E. sepositus* (Entrambasaguas et al. 2008), but all these variables had minor variations in our study and failed to explain sea star abundance in our community. This lack of relationship with environmental variables seems to be common in other echinoderms, whose distributions are better explained by biotic factors (McClanahan 1998; Alves et al. 2001; Dumas et al. 2007).

Community composition varied between locations with high and low abundance of *Echinaster sepositus*. Differences were small as indicated by the low R value found in our ANOSIM analysis and driven primarily by sea urchins, *Sarpa salpa*, crustose coralline algae, sparid fish, and calcareous articulated algae. Among them, abundance of encrusting algae was positively correlated with the abundance of the sea star although the true nature of this association is unknown. Whatever the mechanisms, they seem to operate from local to regional scales as suggested by the high match in the index of dispersion of both species at the multiple scales investigated in our study. Both species

showed a highly contagious distribution up to about 40 km, when they came close to a random distribution.

A possible explanation for the positive relationship between the abundance of *Echinaster sepositus* and crustose coralline algae is that high cover of crustose coralline algae may lead to higher abundance of *E. sepositus*. Numerous benthic invertebrates are known to be positively associated with high cover of crustose coralline algae. Its presence is known to enhance larval settlement and induce metamorphosis in many invertebrates (Daume et al. 1999; Heyward and Negri 1999; Morse et al. 1988) including sea stars (Barker 1977; Johnson and Sutton 1994) and other echinoderms (Huggett et al. 2006). Whether *Echinaster sepositus* settles preferentially on this substrate remains unknown but could be behind this positive association. Crustose coralline algae are also known to enhance growth and survival of new recruits (Rowley 1990; Harrington et al. 2004). A trophic relationship between *Echinaster sepositus* and crustose red algae or its associated fauna could also explain this association. Feeding preferences can result in spatial patterns of predator abundance if the predator mimics an irregular prey distribution or selects for environments that facilitate the access to its food resources (Yasuda and Ishikawa 1999; Torres et al. 2008; Hines et al. 2009). The diet of *E. sepositus* includes algae and multiple meiofaunal groups (Vaserot 1961) although further information is needed to clarify feeding habits and preferences. Crustose coralline algae can host a wide variety of associated fauna (Martín 1987; Williamson and Creese 1996; Cebrian and Uriz 2006), so the possibility that *E. sepositus* could feed on these algae or their associated fauna cannot be ruled out. The sea star *Stichaster australis* is known to feed on the encrusting algae *Mesophyllum insigne* until juveniles reach over 2 cm in diameter (15–18 months old). Experimental testing of the sea star feeding preferences and stable isotopes analysis could provide useful data to support or refute the hypothesis of a trophic link between *E. sepositus* and crustose coralline algae.

An opposite hypothesis would be a positive effect of *Echinaster sepositus* on percent cover of crustose coralline algae. Our experimental data failed to support this hypothesis. The sea star was unable to induce any shift in the composition of the benthic community in 4 months despite we used densities that exceeded over three times the maximum natural density found in our study area. A larger percent cover of crustose coralline algae could result from a true increase in their abundance, a reduction in other algal or sessile species, or a combination of both factors. Although a true increase in crustose coralline algae may need longer than 4 months to be noticeable, we did notice changes in community composition over the course of the experiment. These changes were restricted to our factor 1 (which included organisms with clear seasonal dynamics such as

Dictyota, *Cladophora*, *Falkenbergia*, *Dilophus*, or *Aglaophenia*) and were unrelated to sea star abundance. Many sea stars are voracious feeders that might control their prey abundance and alter community organization and functioning (Menge 1982; Duggins 1983; Rotjan and Lewis 2008). However, *E. sepositus* seems to lack the biological traits that make other echinoderms key players in community organization (Uthicke et al. 2009). Overall, our results suggest against the role of *E. sepositus* as a main contributor to community organization. If any, changes in the sessile community mediated by the sea star must be subtle and need longer to become noticeable.

Alternatively, the positive correlation between crustose coralline algae and *Echinaster sepositus* could reflect a mutual relationship on a third unidentified biotic or abiotic factor. For example, herbivores have the capacity to remove erect fleshy algae exposing crustose coralline algae (Palacin et al. 1998a), which facilitates the abundance of other invertebrates (Cebrian and Uriz 2006). Our data showed that sea urchins and *Sarpa salpa* were the main contributors to the dissimilarities between locations with high and low abundance of *E. sepositus*. Whether herbivores could favor a correlation between sea star abundance and crustose coralline algae by depleting fleshy algae remains an open question subject to hypothesis testing. Similarly, crustose coralline algae and *E. sepositus* could target the same habitat because of specific but unknown abiotic characteristics. For example, temperature is known to have significant effect on species distribution. Our northern locations have larger abundance of sea stars, crustose coralline algae, and may be up to 2°C cooler than our southern locations. Also, northern and southern locations differ in their orientation, predominant wind, and wave exposure, which could account for differences in community composition or species abundance. At this larger geographic scale, we could expect a correlation between sea star abundance and temperature, orientation, or predominant winds if measured. The abundance and patchy distribution of *E. sepositus* in southern Spain is similar to what we report in our study (Sanchez-Jerez et al. 2005, technical report) despite water temperature is about 5°C higher. Although the role of these factors in the abundance of *E. sepositus* is unclear, geographic variation in temperature, or other factors are unlikely to contribute to the striking variation in sea star abundance found between nearby locations. Factors acting at a scale of hundred meters or less are more likely behind the local variation found for this species.

Multiple interacting factors affect the distribution and abundance of species. Understanding their role is crucial to learn how natural communities organize and function. Our study took a comprehensive approach by looking at multiple factors at a within-community level over a regional scale. Our data showed that the within-community spatial

variability in the abundance of *Echinaster sepositus* and crustose coralline algae was correlated. Experimental addition of the sea star resulted in no changes in algal composition. These results suggest that crustose coralline algae could mediate the abundance of *E. sepositus*. Habitat heterogeneity has been suggested to play a major role in the organization of echinoderm assemblages, which showed greater variability at fine than large spatial scales (Entrambasaguas et al. 2008). Our data were consistent with this hypothesis and showed an increasingly larger departure from a random distribution of *E. sepositus* as we stepped down from regional to local scales. Our detailed analysis of shallow Mediterranean algal communities also opened a number of questions that remain to be tested. More research will clarify the true nature of the relationship between crustose coralline algae and *E. sepositus*.

Acknowledgments The present study was funded by the Spanish Ministry of Science and Education (MPA-STAR, grant 200730I005 and MARMOL, CMT2007-66635). Special thanks to N. Viladrich, O. Sacristán, A. Canyelles, and R. Bernardello for technical and field assistance. We are grateful to Patrik Kraufvelin and three anonymous reviewers whose useful comments greatly improved the manuscript. This article is part of Villamor's PhD thesis.

References

- Alves FMA, Chicharo LM, Serrao E, Abreu AD (2001) Algal cover and sea urchin spatial distribution at Madeira Island (NE Atlantic). *Sci Ma* 65:383–392
- Barker MF (1977) Observations on settlement of brachiolaria larvae of *Stichaster australis* (Verrill) and *Coscinasterias calamaria* (Gray) (Echinodermata Asteroidea) in laboratory and on shore. *J Exp Mar Biol Ecol* 30:95–108
- Becerro MA, Goetz G, Paul VJ, Scheuer PJ (2001) Chemical defenses of the sacoglossan mollusk *Elysia rufescens* and its host alga *Bryopsis* sp. *J Chem Ecol* 27:2287–2299
- Benedetti-Cecchi L, Cinelli F (1995) Habitat heterogeneity, sea urchin grazing and the distribution of algae in littoral rock pools on the west-coast of Italy (Western Mediterranean). *Mar Ecol Prog Ser* 126:203–212
- Boudouresque CF (1985) Groupes ecologiques d'algues marines et phytocenoses benthiques en Méditerranée Nord-Occidentale: une revue. *Giorn Bot Ital* 118:7–42
- Britton-Simmons KH (2006) Functional group diversity, resource pre-emption and the genesis of invasion resistance in a community of marine algae. *Oikos* 113:395–401
- Cebrian E, Uriz MJ (2006) Grazing on fleshy seaweeds by sea urchins facilitates sponge *Cliona viridis* growth. *Mar Ecol Prog Ser* 323:83–89
- Chapman MG, Underwood AJ (2008) Scales of variation of gastropod densities over multiple spatial scales: comparison of common and rare species. *Mar Ecol Prog Ser* 354:147–160
- Clarke KR, Ainsworth M (1993) A method of linking multivariate community structure to environmental variables. *Mar Ecol Prog Ser* 92:205–219
- Daume S, Brand-Gardner S, Woelkerling WJ (1999) Settlement of abalone larvae (*Haliotis laevigata* Donovan) in response to non-geniculate coralline red algae (Corallinales, Rhodophyta). *J Exp Mar Biol Ecol* 234:125–143
- Davidowitz G, Rosenzweig ML (1998) The latitudinal gradient of species diversity among North American grasshoppers (Acrididae) within a single habitat: a test of the spatial heterogeneity hypothesis. *J Biogeog* 25:553–560
- Diez I, Santolaria A, Gorostiaga JM (2003) The relationship of environmental factors to the structure and distribution of subtidal seaweed vegetation of the western Basque coast (N Spain). *Estuar Coast Shelf Sci* 56:1041–1054
- Duggins DO (1983) Starfish predation and the creation of mosaic patterns in a kelp dominated community. *Ecology* 58:1218–1236
- Dumas P, Kulbicki M, Chifflet S, Fichez R, Ferraris J (2007) Environmental factors influencing urchin spatial distributions on disturbed coral reefs (New Caledonia, South Pacific). *J Exp Mar Biol Ecol* 344:88–100
- Elliot JM (1977) Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biological Association, UK
- Entrambasaguas L, Perez-Ruzafa A, Garcia-Charton JA, Stobart B, Bacallado JJ (2008) Abundance, spatial distribution and habitat relationships of echinoderms in the Cabo Verde Archipelago (eastern Atlantic). *Mar Freshwater Res* 59:477–488
- Eriksson O (1996) Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. *Oikos* 77:248–258
- Fabricius K, De'ath G (2001) Environmental factors associated with the spatial distribution of crustose coralline algae on the Great Barrier Reef. *Coral Reefs* 19:303–309
- Ferguson JC (1969) Feeding activity in *Echinaster* and its induction with dissolved nutrients. *Biol Bull* 136:374–384
- Garrabou J, Riera J, Zabala M (1998) Landscape pattern indices applied to Mediterranean subtidal rocky benthic communities. *Landscape Ecol* 13:225–247
- Garrabou J, Riera J, Zabala M (2002) Structure and dynamics of north-western Mediterranean rocky benthic communities along a depth gradient. *Estuar Coast Shelf Sci* 55:493–508
- Gili JM, Ros J (1985) Study and cartography of the benthic communities of Medes Islands (NE Spain). *Mar Ecol PSZNI* 6:219–238
- Gotelli NJ, Ellison AM (2004) A primer of ecological statistics. Sinauer, Massachusetts
- Grace JB (1999) The factors controlling species density in herbaceous plant communities: an assessment. *Perspect Plant Ecol Evol Syst* 2:1–28
- Harmelin-Vivien M, Le Direach L, Bayle-Sempere J, Charbonnel E, Garcia-Charton JA, Ody D, Perez-Ruzafa A, Renones O, Sanchez-Jerez P, Valle C (2008) Gradients of abundance and biomass across reserve boundaries in six Mediterranean marine protected areas: evidence of fish spillover? *Biol Conserv* 141:1829–1839
- Harrington L, Fabricius K, De'ath G, Negri A (2004) Recognition and selection of settlement substrata determine post-settlement survival in corals. *Ecology* 85:3428–3437
- Helmuth B, Broitman BR, Blanchette CA, Gilman S, Halpin P, Harley CDG, O'Donnell MJ, Hofmann GE, Menge B, Strickland D (2006) Mosaic patterns of thermal stress in the rocky intertidal zone: implications for climate change. *Ecol Monogr* 76:461–479
- Hereu B (2006) Depletion of palatable algae by sea urchins and fishes in a Mediterranean subtidal community. *Mar Ecol Prog Ser* 313:95–103
- Hereu B, Zabala M, Sala E (2008) Multiple controls of community structure and dynamics in a sublittoral marine environment. *Ecology* 89:3423–3435
- Hewitt JE, Thrush SE, Halliday J, Duffy C (2005) The importance of small-scale habitat structure for maintaining beta diversity. *Ecology* 86:1619–1626
- Heyward AJ, Negri AP (1999) Natural inducers for coral larval metamorphosis. *Coral Reefs* 18:273–279
- Himmelman JH, Dutil C (1991) Distribution, population structure and feeding of subtidal seastars in the northern Gulf of St. Lawrence. *Mar Ecol Prog Ser* 76:61–72

- Hines AH, Long WC, Terwin JR, Thrush SF (2009) Facilitation, interference, and scale: the spatial distribution of prey patches affects predation rates in an estuarine benthic community. *Mar Ecol Prog Ser* 385:127–135
- Hubbell SP, Ahumada JA, Condit R, Foster RB (2001) Local neighborhood effects on long-term survival of individual trees in a neotropical forest. *Ecol Res* 16:859–875
- Huggett MJ, Williamson JE, de Nys R, Kjelleberg S, Steinberg PD (2006) Larval settlement of the common Australian sea urchin *Heliocidaris erythrogramma* in response to bacteria from the surface of coralline algae. *Oecologia* 149:604–619
- Hyman LH (1955) The invertebrates: echinodermata: the coelomate Bilateria. International Books & Periodicals Supply Services, Delhi
- Izsak C, Price ARG (2001) Measuring beta-diversity using a taxonomic similarity index, and its relation to spatial scale. *Mar Ecol Prog Ser* 215:69–77
- Johnson CR, Sutton DC (1994) Bacteria on the surface of crustose coralline algae induce metamorphosis of the crown-of-thorns starfish *Acanthaster Planci*. *Mar Biol* 120:305–310
- Keddy PA (1992) A pragmatic approach to functional ecology. *Funct Ecol* 6:621–626
- Littler MM, Littler DS (1984) Relationships between macroalgal functional form groups and substrata stability in a sub-tropical rocky-intertidal system. *J Exp Mar Biol Ecol* 74:13–34
- Maldonado M, Uriz MJ (1998) Microrefuge exploitation by subtidal encrusting sponges: patterns of settlement and post-settlement survival. *Mar Ecol Prog Ser* 174:141–150
- Martín D (1987) Anélidos poliquetos asociados a las concreciones de algas calcáreas del litoral catalán. *Miscel Zool* 11:61–75
- Mas Cornet G (2005) Proyecto de reintroducción del tritón marino en la Costa Brava. Manual de manejo en cautividad. Centro de Estudios del Mar de Begur-NEREO. <http://www.nereo.org/images/corn/Manual%20de%20manejo%20en%20cautividad.pdf>
- McClanahan TR (1998) Predation and the distribution and abundance of tropical sea urchin populations. *J Exp Mar Biol Ecol* 221:231–255
- Menge BA (1982) Effects of feeding on the environment: Asteroidea. In: Jangoux M, Lawrence JM (eds) Echinoderm nutrition. Balkema, Rotterdam, pp 521–551
- Moran MD (2003) Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos* 100:403–405
- Morse DE, Hooker N, Morse ANC, Jensen RA (1988) Control of larval metamorphosis and recruitment in sympatric agariciid corals. *J Exp Mar Biol Ecol* 116:193–217
- Ocaña Martín A, Sánchez Tocino L, López González S, Viciano Martín JF (2000) Guía submarina de invertebrados no artrópodos, 2ª Edición. Editorial Comares, Granada
- Palacin C, Giribet G, Carner S, Dantart L, Turon X (1998a) Low densities of sea urchins influence the structure of algal assemblages in the western Mediterranean. *J Sea Res* 39:281–290
- Palacin C, Turon X, Ballesteros M, Giribet G, López S (1998b) Stock evaluation of three littoral echinoid species on the Catalan coast (North-Western Mediterranean). *Mar Ecol PSZNI* 19:163–177
- Pérès JM, Picard JN (1964) Nouveau manuel de bionomie benthique de la Mer Méditerranée. *Rec Trav St MarEndoume* 31:1–137
- Perner J, Voigt W (2007) Measuring the complexity of interaction webs using vertical links between functional groups. *Agr Ecosyst Environ* 120:192–200
- Riedl R (1983) Fauna y Flora del Mar Mediterráneo. Ediciones Omega, Barcelona
- Rilov G, Schiel DR (2006) Seascape-dependent subtidal-intertidal trophic linkages. *Ecology* 87:731–744
- Risk MJ (1972) Fish diversity on a coral reef in the Virgin Islands. *Atoll Res Bull* pp 1–6
- Roberts DE, Cummins SP, Davis AR, Chapman MG (2006) Structure and dynamics of sponge-dominated assemblages on exposed and sheltered temperate reefs. *Mar Ecol Prog Ser* 321:19–30
- Ros JD, Romero J, Ballesteros E, Gili JM (1985) Diving in blue water. The benthos. In: Margalef R (ed) Western Mediterranean. Pergamon Press, London, pp 233–295
- Rotjan RD, Lewis SM (2008) Impact of coral predators on tropical reefs. *Mar Ecol Prog Ser* 367:73–91
- Rowley RJ (1990) Newly settled sea urchins in a kelp bed and urchin barren ground - a comparison of growth and mortality. *Mar Ecol Prog Ser* 62:229–240
- Ruitton S, Francour P, Boudouresque CF (2000) Relationships between algae, benthic herbivorous invertebrates and fishes in rocky sublittoral communities of a temperate sea (Mediterranean). *Estuar Coast Shelf Sci* 50:217–230
- Sarà M, Vacelet J (1973) Écologie des Démosponges. In: Grasse PP (ed) *Traité de zoologie (anatomie, systématique, biologie)*. Masson & Cie, Paris, pp 462–576
- SPSS (1999) *Systat 9: statistics I*. SPSS Inc, Chicago
- Steneck RS, Watling L (1982) Feeding capabilities and limitation of herbivorous molluscs: a functional group approach. *Mar Biol* 68:299–319
- Tabachnick BG, Fidell LS (2001) *Using multivariate statistics*. Allyn & Bacon, Needham Heights
- Tilman D (1985) The resource-ratio hypothesis of plant succession. *Am Nat* 125:827–852
- Tilman D (1994) Competition and biodiversity in spatially structured habitats. *Ecology* 75:2–16
- Torres LG, Read AJ, Halpin P (2008) Fine-scale habitat modelling of a top marine predator: do prey data improve predictive capacity? *Ecol Appl* 18:1702–1717
- Tuya F, Haroun RJ (2006) Spatial patterns and response to wave exposure of shallow water algal assemblages across the Canarian Archipelago: a multi-scaled approach. *Mar Ecol Prog Ser* 311:15–28
- Underwood AJ, Chapman MG (1996) Scales of spatial patterns of distribution of intertidal invertebrates. *Oecologia* 107:212–224
- Uthicke S, Schaffelke B, Byrne M (2009) A boom-bust phylum? Ecological and evolutionary consequences of density variations in echinoderms. *Ecol Monogr* 79:3–24
- Vassero J (1961) Caractère hautement spécialisé du régime alimentaire chez les astérides *Echinaster sepositus* et *Henricia sanguinolenta*, prédateurs de spongiaires. *Bull Soc Zool Fr* 86:796–809
- Virgilio M, Airoidi L, Abbiati M (2006) Spatial and temporal variations of assemblages in a Mediterranean coralligenous reef and relationships with surface orientation. *Coral Reefs* 25:265–272
- Westfall PH, Young SS (1993) On adjusting *P*-values for multiplicity. *Biometrics* 49:941–944
- Williamson JE, Creese RG (1996) Small invertebrates inhabiting the crustose alga *Pseudolithoderma* sp (Ralfsiaceae) in northern New Zealand. *New Zeal J Mar Freshw* 30:221–232
- Yasuda H, Ishikawa H (1999) Effects of prey density and spatial distribution on prey consumption of the adult predatory ladybird beetle. *J Appl Entomol* 123:585–589
- Zajac RN, Lewis RS, Poppe LJ, Twichell DC, Vozarik J, DiGiacomo-Cohen ML (2003) Responses of infaunal populations to benthoscape structure and the potential importance of transition zones. *Limnol Oceanogr* 48(2):829–842