

Spatial variability and human disturbance in shallow subtidal hard substrate assemblages: a regional approach

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ABSTRACT: Quantitative information about spatial patterns in subtidal hard substrate assemblages is scant. Such information is necessary to understand the responses to anthropogenic disturbances in these habitats. Along the coast of Apulia (Southern Italy), the collection of the European date mussel *Lithophaga lithophaga* is a strong source of disturbance: harvesting is carried out by demolition of the rocky substrate and causes epibiota disappearance. A hierarchical sampling design was used to quantify the spatial variability of subtidal epibenthic assemblages and the extent of rock damage due to *L. lithophaga* harvesting along 360 km of rocky coasts in Apulia. The surveyed coast was divided into 8 adjacent sectors, and replicate samples were taken by visual inspection at each of the 3 sites nested in each sector. Multivariate analyses indicated that assemblages differed consistently with spatial scale, variability being higher at the largest scale. However, variability among sites within each sector was also detected. Patchiness (i.e., average similarity among quadrats) was consistent among sectors. Some species were identified as 'important' in characterising and/or differentiating sectors. The pattern of distribution of these species as well as total cover and number of species were analysed by analysis of variance. Results recorded a considerable source of variation at site level. Damage by *L. lithophaga* fishing was shown to be extremely widespread. A humped relationship between patchiness and disturbances by *L. lithophaga* fisheries was obtained. In particular, patchiness at a small scale was highest at 'intermediate' levels of damage, because disturbance produces patches of different size and/or age, leading to 'mosaic' landscapes of epibenthic assemblages.

KEY WORDS: Subtidal assemblage · Spatial scale · Human disturbance · Rocky substrate · *Lithophaga lithophaga* · Mediterranean Sea

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INTRODUCTION

The change in environmental conditions and the impact of human activities can be the main causes of landscape heterogeneity at different scales, from local patchiness to variation along climatic gradients (Levin

1992, Tilman & Kareiva 1997). Linkage across multiple scales is increasingly considered by ecologists (Peterson & Parker 1998). The proposal of macroecology (Brown 1995, Maurer 1999) as a way to reconcile biogeography and ecology mainly focuses on terrestrial habitats (Boero 1999). Its rationale should be equally applicable to marine environments. The complementary vision of landscape ecology is again primarily interested in terrestrial environment (Forman & Godron

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1986, Farina 1998), but the application of these concepts to the sea is timely (Cocito et al. 1991, Garrabou et al. 1998a, Smith & Witman 1999).

The most obvious distribution pattern of hard substrate marine communities is vertical zonation, which is often explained with the variation of environmental factors such as light (Pérès 1982) or water movement (Riedl 1971). Attention towards abiotic factors characterised the continental-European approach, whereas British and American ecologists, often dealing with intertidal communities only (Connolly & Roughgarden 1999), mainly invoked biotic interactions to explain community patterns. Following Dunson & Travis (1991), Barry & Dayton (1991) re-appraised the ecological importance of physical factors in the organisation of marine communities. Since competition operates at a more local scale than climate, consideration of scale is a way to reconcile the 2 approaches.

The large-scale distribution of subtidal marine biota mostly concerns biogeography and has rarely been linked to ecological features, especially in the case of rocky substrates. Many modern studies of ecological patterns concentrate on small-scale structuring processes, such as competition and predation, or local heterogeneity within habitat (Chapman 1994, Thompson et al. 1996, Benedetti-Cecchi et al. 1999). Whilst the need to detect community variability at different spatial scales is widely recognised (Butler & Chesson 1990, Hewitt et al. 1998), few studies of marine hard substrata have explicitly embraced a hierarchy of spatial scales (Glasby 1999). Most information derives from the intertidal (Paine et al. 1985, Underwood & Chapman 1996, 1998a,b, Benedetti-Cecchi et al. 2000); but, in the constantly submerged subtidal, the influence of gradients of spatial scales larger than tens of metres on biodiversity is a growing field of interest (Kennelly & Underwood 1993, Chapman et al. 1995, Cornell & Karlson 1996, Roberts 1996, Guichard & Bourget 1998, Hughes et al. 1999, Smith & Witman 1999). The scant information available on the subtidal means that possible linkages between large- and small-scale processes, in areas from patches to landscapes, are poorly understood. Probably, the paucity of data available on this topic is also linked to the fact that large-scale research in the subtidal is expensive and severely time-limited by logistics.

Subtidal rocky substrates of the Mediterranean Sea are intensively used by humans for a number of activities, which range from seafood collection to diving tourism (Garrabou et al. 1998b). A high percentage of the coast of Apulia (South-Eastern Italy, between the Southern Adriatic and Ionian Seas) is of great significance in social-economic terms for fisheries and tourism. The coast of Apulia is several hundreds of km long (Fig. 1) and is characterised by long rocky

stretches, separated by sandy beaches. The geographic position and variety of the coast make the subtidal communities of Apulia extremely varied in terms of species composition and biogeographic affinities (Bedulli et al. 1986, Damiani et al. 1988).

Two surveys carried out in the last 10 yr (Fanelli et al. 1994) revealed that Apulian rocky subtidal habitats are continuously subjected to the intensive human predation on the European date mussel *Lithophaga lithophaga*. Date mussel collection requires breaking of rocks to expose the molluscs, causing the destruction of the epibiota (Russo & Cicogna 1992, Fanelli et al. 1994). This leads to either complete desertification or 'mosaic' landscapes of epibenthic assemblages. The importance of this phenomenon was remarked on by Naylor (1995), while Dayton et al. (1995) and Hall (1999) cited it as a prime example of fishery disturbance on subtidal hard substrates.

During the spring of 1997, we surveyed the rocky coasts of Apulia, analysing the subtidal sessile epibiota across spatial scales ranging from metres to hundreds of km. A hierarchical sampling design provided a framework for quantifying the variation among samples due to each spatial scale (Underwood 1997). We chose to sample subvertical rocky walls at about 5 m depth, usually characterised by more or less diverse algal assemblages (Pérès 1982).

The present paper describes tests of hypotheses about spatial distribution of such epibenthic assemblages. Disturbance, however, plays a major role in creating different patterns of change from place to place (Connell & Sousa 1983, Airoidi 1998). Thus, in addition, the study evaluates the extent of rock damage due to *L. lithophaga* fisheries and how this form of disturbance could play a role in influencing the pattern of natural variability of epibenthic assemblages.

Most published studies focus on the spatial variation of mean abundance of either individual species, sets of interacting species, or so-called functional groups of species. Here the spatial variability has been evaluated considering the pattern of distribution of species richness, total cover, community structure (i.e., qualitative species composition), and 'important' taxa (i.e., those whose relative cover characterises and/or differentiates assemblages).

METHODS

Study sites and sampling. From 12 to 23 May 1997, a survey from Peschici (41° 57' N, 16° 00' E) to Taranto (40° 24' N, 17° 12' E), Southern Italy, was carried out, covering most of the Apulian coast. The surveyed area was divided into 650 sections of 1 km each, and only the 360 sections with rocky substrates were consid-

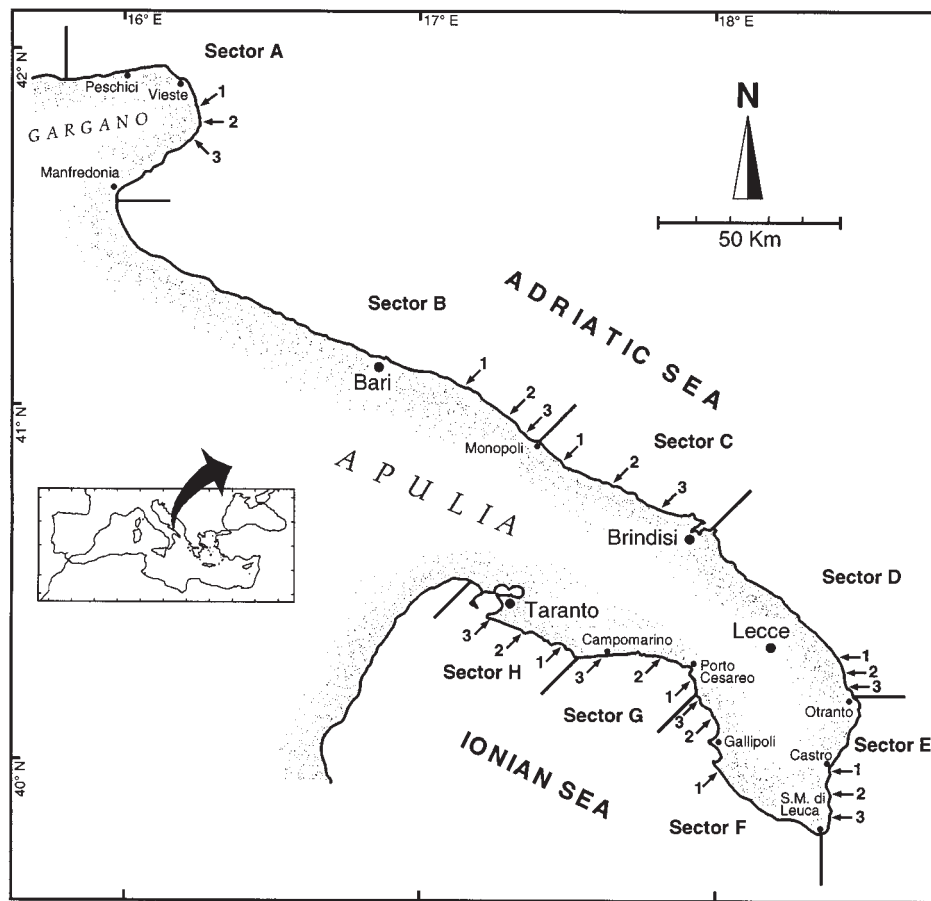


Fig. 1. Surveyed coast and its positioning in the Mediterranean region. The sampling sites (1 to 3), randomly selected among rocky substrate sections within each of the 8 sectors (A to H), are shown

ered. These were grouped into 8 adjacent sectors, having unequal total length because of different proportions of sandy and rocky bottoms, but all including 45 rocky sections. In each sector, 3 sampling sites were randomly selected out of the 45 sections (Fig. 1). Subtidal sessile epibiota was investigated by visual estimation of 3 random quadrats on sub-vertical rocky surfaces at about 5 m depth. Thus, 3 spatial scales were considered: small (2 to 15 m), variation between quadrats at each site; intermediate (3 to 21 km), variation between sites within sectors; and broad (45 to 500 km), variation between sectors.

A single team of 5 researchers performed sampling operations. Sampling quadrats were 1 m² divided into 25 equal squares. The percent substrate cover by conspicuous organisms was quantified by giving each individual taxon a score ranking from 0 to 4 in each smaller square, and then adding up scores for all the smaller squares where the taxon was present. Final values were expressed as percentages. Organisms filling less than 1/4 square were given an arbitrary

value of 0.5 (Dethier et al. 1993). Conspicuous organisms were directly recognised in the field; specimens were collected for later identification only when in doubt.

At each site, the presence of date mussels (as living specimens or as empty galleries) was recorded. The impact of *Lithophaga lithophaga* fisheries was assessed in 5 randomly selected surfaces of 10 × 2 m. Rock damage measurements were obtained by considering the size and frequency of disturbed patches (e.g., evident breaks in the rocks). For each sampling surface a score ranging from 0 to 7 was assigned following the damage evaluation categories reported in Fanelli et al. (1994). Observed values were then divided by 7 to relate the observed damage to the maximum possible damage, obtaining a weighted index of rock damage (D_w) ranging between 0 (absence of damage) and 1 (complete desertification).

Statistical analysis. Spatial patterns of total cover and species richness were examined by 2-way ANOVA (GMAV5, University of Sydney). Sectors were

considered as random factors, sites were randomly nested in sectors, and quadrats provided 3 replicates. The homogeneity of variance was tested by Cochran's test (C) (Underwood 1997).

Analysis of similarities (ANOSIM, Clarke 1993) was used to compare community structure within and among sectors, under the hypothesis that assemblages differ at the broad spatial scale (among sectors) but not at the smaller spatial scale within each sector (among sites). Comparisons were based on Bray-Curtis similarity values (S_{BC}) (Bray & Curtis 1957) calculated on all taxa within each quadrat (PRIMER, Plymouth Marine Laboratory, Clarke 1993). Data were fourth root transformed to arrange all organisms in the same range of abundance.

To test the hypothesis of higher similarities among sites within the same sector than among sites from different sectors, the mean dissimilarities among sites in each sector ($1 - S_{BC}$) were compared to the average dissimilarity (and 95% confidence limits) among the remaining sectors. Differences among sectors, as well as among sites within each sector, were represented by non-metric multidimensional scaling ordinations (MDS), considering site centroids (the mean cover values of each taxon in the 3 replicate quadrats of each site) and sector centroids (the mean cover values of each taxon in the 3 sites of each sector). Stress values were shown for each MDS plot to indicate the goodness of representation of differences among samples.

The average dissimilarity within a site was used to measure variability among replicate quadrats. ANOVA was performed to test the hypothesis that variability within sites (i.e., community patchiness) differed among sectors. Sectors were random factors, and sites provided 3 replicate readings.

SIMPER (Clarke 1993) was used to identify 'important' taxa. These had covers that contributed more than 10% to similarity among sites within each sector and/or that accounted for at least 5% of the average dissimilarity among sectors. The spatial patterns of these important taxa were examined using ANOVA. In some cases, the variances of species cover did not meet the assumption of homogeneity ($p > 0.05$). Nevertheless, since ANOVA is considered sufficiently robust to the departures from the assumption, the analyses were still interpreted with the more conservative probability level of 0.01 (Underwood 1997).

Spatial patterns of rock damage were examined using 2-way ANOVA to test for differences among and within sectors. To test for relationship between community patchiness and rock damage, values of dissimilarity within sites ($1 - S_{BC}$) were plotted against the values of D_w averaged for each site. This relationship was described by polynomial regression.

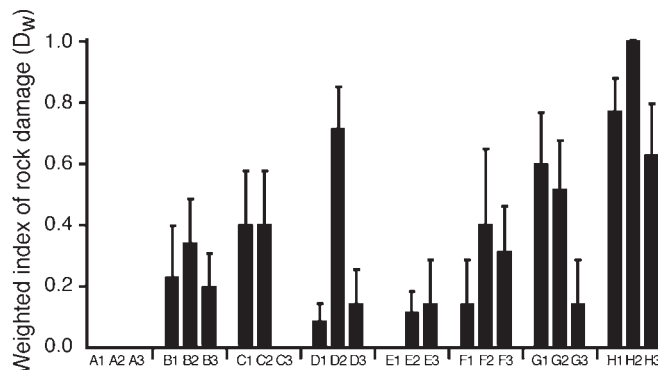


Fig. 2. Spatial pattern of weighted index of rock damage (D_w) (mean \pm SE, $n = 5$)

RESULTS

Disturbance by date mussel fisheries

The 3 sites of Sector A (Gargano peninsula) were unaffected by date mussel fisheries, possibly because substrate or other conditions are not suitable for abundant date mussel settlement. Rock damage due to *Lithophaga lithophaga* fisheries was widespread in most of the remaining 21 sites suitable for date mussel settlement (mean $D_w = 0.35$, SE = 0.06, $n = 21$). Significant differences were detected among sectors (2-way ANOVA, $F_{7,16} = 3.51$, $p < 0.05$). Sector H showed the highest values of rock damage (mean $D_w = 0.80$ SE = 0.11, $n = 3$), whilst the lowest damage was recorded in Sector E (mean $D_w = 0.09$ SE = 0.04, $n = 3$) (Fig. 2). Rock damage varied significantly also among sites within sectors ($F_{16,48} = 2.26$, $p < 0.05$).

Substrate cover

The total amount of substrate covered by algae and sessile animals ranged from 12 to 96%, with a global average value of 52.8% (SE = 2.2, $n = 72$). Cover did not vary significantly among sectors (2-way ANOVA, $F_{7,16} = 1.25$, $p > 0.05$). Significant differences were found among sites within sectors ($F_{16,48} = 3.29$, $p < 0.001$).

Species richness

A total of 91 taxa were recognised in the field (Table 1). Almost all taxa were identified to species level, except for a few groups in which a consistent species distinction in all quadrats turned out to be impossible. Later examination of voucher specimens meant that the identified group 'Encrusting calcified

Table 1. Taxonomic list of the species (or species groups) recorded

Rhodophyceae	Porifera (continued)
Filamentous red algae	<i>Haliclona</i> sp.
Encrusting calcified red algae	<i>Hemimycale columella</i> (Bowerbank)
<i>Amphiroa</i> sp.	<i>Ircinia oros</i> (Schmidt)
<i>Corallina elongata</i> Ellis et Solander	<i>Ircinia variabilis</i> (Schmidt)
<i>Haliptilon virgatum</i> (Zanardini) Garbary et Johansen	<i>Peraplysilla spinifera</i> Schulze
<i>Dudresnaya verticillata</i> (Withering) Le Jolis	<i>Petrosia ficiformis</i> (Poiret)
<i>Jania rubens</i> (L.) Lamouroux	<i>Phorbas fictitius</i> (Bowerbank)
<i>Laurencia obtusa</i> (Hudson) Lamouroux	<i>Phorbas tenacior</i> (Topsent)
<i>Liagora viscida</i> (Forsskål) C. Agardh	<i>Tethya aurantium</i> (Pallas)
<i>Peyssonnelia dubyi</i> Crouan et Crouan	Hydrozoa
<i>Peyssonnelia squamaria</i> (Gmelin) Decaisne	Hydroids
<i>Scinia furcellata</i> (Turner) J. Agardh	Anthozoa
<i>Sphaerococcus coronopifolius</i> Stackhouse	<i>Aiptasia mutabilis</i> (Gravenhorst)
Phaeophyceae	<i>Anemonia viridis</i> (Forsskål)
Filamentous brown algae	<i>Balanophyllia europaea</i> (Risso)
<i>Colpomenia sinuosa</i> (Mertens) Derbs et Solier	<i>Cereus pedunculatus</i> (Pennant)
<i>Cystoseira compressa</i> (Esper) Gerloff et Nizamuddin	<i>Cladocora caespitosa</i> (L.)
<i>Dictyopteris polypodioides</i> (De Candolle) Lamouroux	<i>Corynactis viridis</i> Allman
<i>Dictyota dichotoma</i> (Hudson) Lamouroux	<i>Maasella edwardsi</i> Lacaze-Duthiers
<i>Dictyota spiralis</i> Montagne	<i>Parazoanthus axinellae</i> (Schmidt)
<i>Stypocaulon scoparium</i> (L.) Kützing	Polychaeta
<i>Padina pavonica</i> (L.) Thivy	Serpulids
<i>Pseudolithoderma adriaticum</i> (Hauck) Verlaque	Bivalvia
<i>Sargassum vulgare</i> C. Agardh	<i>Mytilus galloprovincialis</i> Lamarck
<i>Zanardinia prototypus</i> (Nardo) Nardo	<i>Ostrea edulis</i> L.
Chlorophyceae	<i>Spondylus gaederopous</i> L.
Filamentous green algae	Gastropoda
<i>Acetabularia acetabulum</i> (L.) Silva	<i>Serpulorbis arenaria</i> (L.)
<i>Anadyomene stellata</i> (Wulfen) C. Agardh	<i>Vermetus triquetrus</i> Ant. Bivona
<i>Cladophora</i> sp.	Cirripedia
<i>Codium bursa</i> (L.) C. Agardh	<i>Balanus perforatus</i> Bruguière
<i>Codium effusum</i> (Rafinesque) Delle Chiaje	Bryozoa
<i>Codium vermilara</i> (Olivieri) Delle Chiaje	<i>Calpensia nobilis</i> (Esper)
<i>Flabellia petiolata</i> (Turra) Nizamuddin	<i>Fron dipora verrucosa</i> (Lamouroux)
<i>Halimeda tuna</i> (Ellis et Solander) Lamouroux	<i>Myriapora truncata</i> (Pallas)
<i>Palmophyllum crassum</i> (Naccari) Rabenhorst	<i>Reptadeonella violacea</i> Johnston
<i>Ulva laetevirens</i> C. Agardh	<i>Schizoporella longirostris</i> Hincks
<i>Valonia macrophysa</i> Kützing	<i>Scrupocellaria reptans</i> (L.)
Porifera	<i>Sertella septentrionalis</i> Harmer
<i>Acanthella acuta</i> Schmidt	Ascidacea
<i>Aplysina aerophoba</i> Schmidt	<i>Aplidium conicum</i> Olivieri
<i>Axinella cannabina</i> (Esper)	<i>Aplidium proliferum</i> (Milne-Edwards)
<i>Axinella polypoides</i> Schmidt	<i>Botryllus schlosseri</i> (Pallas)
<i>Chondrilla nucula</i> Schmidt	<i>Cystodites dellechiajei</i> (Della Valle)
<i>Chondrosia reniformis</i> Nardo	<i>Didemnum maculosum</i> (Milne-Edwards)
<i>Cliona celata</i> Grant	<i>Diplosoma listerianum</i> (Milne-Edwards)
<i>Cliona copiosa</i> Sarà	<i>Halocynthia papillosa</i> (L.)
<i>Cliona rhodensis</i> Rutzler et Bromley	<i>Microcosmus</i> sp.
<i>Cliona viridis</i> (Schmidt)	<i>Perophora viridis</i> Verrill
<i>Crambe crambe</i> (Schmidt)	<i>Polysyncraton lacazei</i> (Giard)
<i>Guancha lacunosa</i> (Johnston)	
<i>Halichondria panicea</i> (Pallas)	

red algae' included at least the species *Lithophyllum frondosum* (Dufour) Furnari, Cormaci et Alongi, *Lithophyllum incrustans* Philippi, *Mesophyllum alternans* (Foslie) Cabioch & Mendoza and *Peyssonnelia polymorpha* (Zanardini) Schmitz. Similarly, *Aglaophenia*

tubiformis Marktanner-Turneretscher, *Eudendrium capillare* Alder, *Eudendrium ramosum* (L.), *Plumularia* sp., *Sertularella ellisi* (Deshayes et Milne-Edwards), *Syntheticium evansi* (Ellis et Solander) and *Ventromma halecioides* (Alder) were recognised within the group

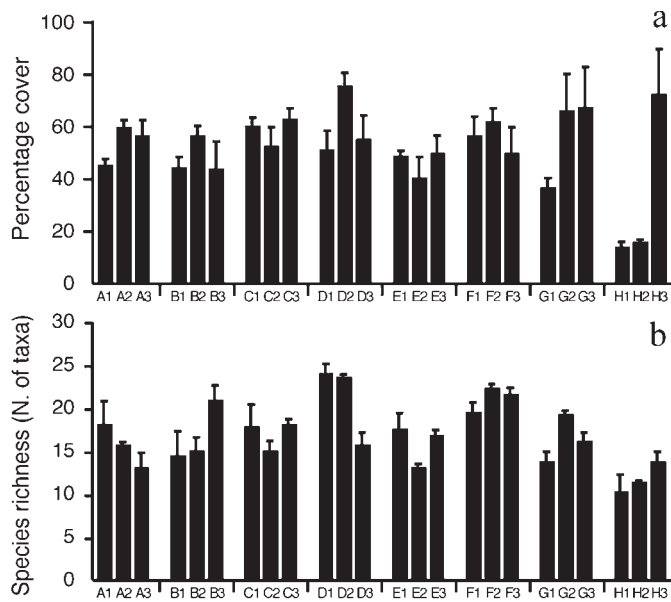


Fig. 3. Spatial pattern of (a) percentage substratum cover (mean \pm SE, $n = 3$) and (b) species richness (mean number of taxa \pm SE, $n = 3$)

'Hydroids', and *Hydroides pseudouncinatus* Zibrowius, *Pomatoceros triqueter* (L.), *Protula tubularia* (Montagu), *Serpula vermicularis* L. and *Vermiliopsis striaticeps* (Grube) within the 'Serpulids'. These identifications bring the number of species recorded to (at least) 102. No attempt to identify filamentous algae was made.

The number of taxa per quadrat ranged from 7 to 26, with an overall mean of 16.8 (SE = 0.5, $n = 72$). Species richness varied both among (2-way ANOVA, $F_{7,16} = 3.59$, $p < 0.05$) and within sectors ($F_{16,48} = 3.36$, $p < 0.001$). The richest site was D1, the poorest H1 (Fig. 3b).

Community structure

The null hypothesis that community structure was similar at all sectors was rejected (ANOSIM, $R = 0.58$, $p < 0.001$). This is also shown by the ordination of sector centroids by MDS, representing differences among assemblages from sector to sector when variability among sites and among quadrats is ignored. All sectors are well separated from each other, except for Sectors F and G, which are characterised by an overlap in similarity (Fig. 4a). A geographical trend is also singled out, the highest distance being between Sector A (Adriatic Sea) and Sector H (Ionian Sea), passing through the sectors between them.

As observed for sectors, the null hypothesis that community structure was similar at all sites was

Table 2. Significant differences in community structure (ANOSIM) among sites in each sector ($n = 3$ quadrats per site; * $p < 0.05$; ** $p < 0.01$)

Sector	Significance
A	**
B	**
C	**
D	*
E	*
F	*
G	*
H	**

Table 3. Average dissimilarity in community structure ($1 - S_{BC}$) among sites within each sector and average dissimilarity (with 95% confidence limits, CL, in parenthesis) between each sector and all the remaining ones

Sector	Dissimilarity among sites within sector	Dissimilarity with remaining sectors
A	56.3	75.8 (4)
B	50.9	68.9 (4)
C	40.0	64.2 (4)
D	52.7	64.5 (4)
E	54.2	70.1 (4)
F	53.3	65.0 (5)
G	53.1	66.7 (5)
H	61.3	69.9 (5)

rejected (ANOSIM, $n = 3$ quadrats per site, $R = 0.90$, $p < 0.001$). ANOSIM performed on each sector also detected significant differences among sites (Table 2).

The MDS representation of site centroids suggested a higher variability among sites in Sectors A, F, G and H (Fig. 4b). However, dissimilarity among sites within each sector was always smaller than the mean dissimilarity between the same sectors and the remaining ones (Table 3).

When expressed as average dissimilarities among replicate quadrats within each site (see 'Methods'),

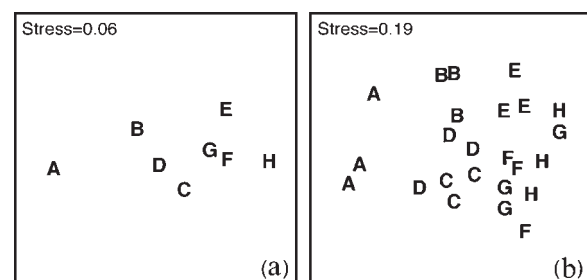


Fig. 4. Non-metric multidimensional scaling ordinations of (a) sector centroids and (b) site centroids

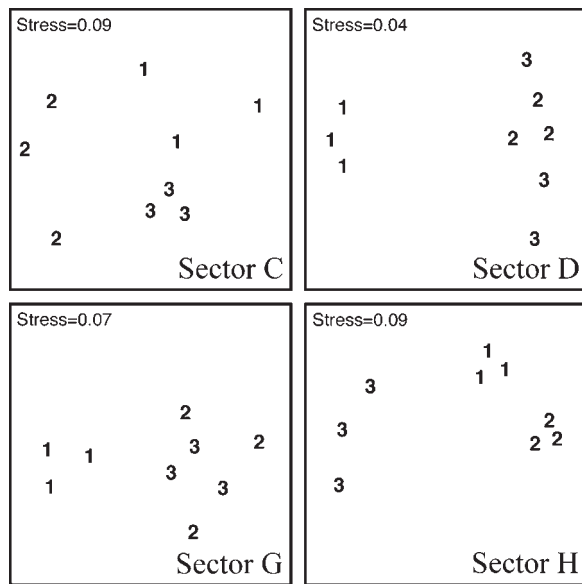


Fig. 5. Non-metric multidimensional scaling ordinations of individual quadrats in 4 selected sectors

patchiness was similar across sectors (1-way ANOVA, $F_{7,16} = 1.57$, $p > 0.05$); but, in each sector, MDS of individual quadrats evidenced different levels of patchiness at different sites. The clearest examples of these different levels of patchiness were found in Sectors C, D, G and H (Fig. 5). Quadrats were more clearly grouped at sites with either the lowest (e.g., C3) or the highest values (e.g., H2) of D_w . The possibility of a humped relationship between community patchiness and disturbance by date mussel fisheries was tested by plotting dissimilarity values calculated for each site against the corresponding D_w values and fitting the plot with a second-order polynomial. This showed that the highest level of dissimilarity within sites (i.e., highest patchiness) corresponded to intermediate levels of rock damage (Fig. 6).

Important taxa

Despite the large number of recorded taxa, SIMPER identified only 14 important taxa in characterising and/or differentiating sectors. Encrusting calcified red algae were important in all sectors, whereas the importance of the other 13 taxa varied greatly. *Peyssonnelia squamaria*, *Chondrosia reniformis* and *Schizoporella longirostris* were important in Sector A (Gargano Promontory). In the Southern Adriatic sectors, *Cereus pedunculatus* was important in Sector B, *P. squamaria* and *Halimeda tuna* in Sector C, and *Calpensia nobilis* in Sector D. In the Ionian sectors, filamentous brown

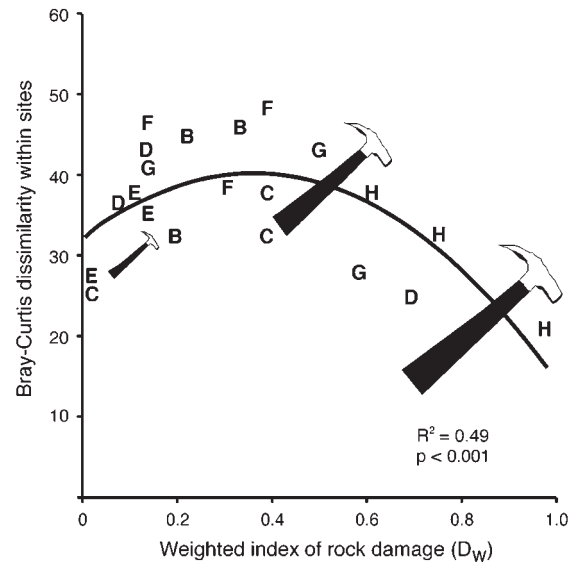


Fig. 6. Relationship between community patchiness (represented by the dissimilarity values for each site) and weighted index of rock damage (D_w). The size of the sledge hammers is roughly proportional to the intensity of the disturbance caused by *Lithophaga lithophaga* fisheries

algae and *Phorbas fictitus* were important in Sector E, and *C. nobilis* in Sectors F and G. In Sector G, serpulids and *Crambe crambe* were also important. The important species of Sector H were *Balanophyllia europaea* and *C. crambe* (Table 4).

The cover of important taxa had different patterns along the coast (Fig. 7). Only encrusting calcified red algae *Crambe crambe* and *Schizoporella longirostris* showed significant cover variations among sectors. Almost all important taxa, apart from encrusting calcified red algae, filamentous brown algae, *C. crambe*, *Chondrosia reniformis* and *Cladocora caespitosa*, showed significant cover variations among sites within sectors. Cover variations both among and within sectors were found only for *S. longirostris* (Table 5).

DISCUSSION

The structure of assemblages varied with greater differences at greater observation scales. Results are also in accordance with the geographical trends of the surveyed coast and could support the hypothesis of Carlile et al. (1989) that communities differ consistently with the latitudinal gradient, probably reflecting biogeographic differences. Studies on intertidal and coral communities, however, report that neighbouring sites differed more from each other than from far apart ones (Underwood & Chapman 1996, Hughes et al. 1999, Smith & Witman 1999). This is likely to be

Table 4. Important taxa, contributing to similarity among sites for each sector (characterisation of sectors) and/or dissimilarity among sectors (differentiation of sectors). Values of similarity $\geq 10\%$ (in the first case) and of dissimilarity $\geq 5\%$ (in the second case) are given in **bold**

Taxon	Code	Characterization of sectors Similarity values (S_{BC})								Differentiation among sectors Dissimilarity values ($1 - S_{BC}$)							
		A	B	C	D	E	F	G	H	A	B	C	D	E	F	G	H
Encrusting calcified red algae	Ecr	12	24	13	20	26	16	15	28	3	4	2	2	3	2	3	3
<i>Halimeda tuna</i>	Htu	0	0	15	8	0	3	11	9	4	4	5	5	4	4	5	5
<i>Peyssonellia squamaria</i>	Psq	14	3	16	7	0	3	1	0	5	4	6	4	4	3	4	4
<i>Calpensia nobilis</i>	Cno	0	2	1	10	1	15	15	4	3	3	3	4	3	5	4	4
Filamentous brown algae	Fib	0	0	1	0	10	5	0	0	1	2	3	2	5	4	2	2
<i>Dictyota dichotoma</i>	Ddi	2	0	11	5	6	6	1	4	3	3	4	3	3	3	3	4
<i>Crambe crambe</i>	Ccr	5	0	2	3	4	5	11	15	2	3	3	3	3	3	3	3
Serpulids	Ser	0	11	5	6	6	6	12	2	3	2	2	2	2	2	2	3
<i>Phorbis fictitius</i>	Pfi	0	11	0	5	13	2	0	0	2	4	2	3	4	2	2	3
<i>Chondrosia reniformis</i>	Cre	11	3	9	2	0	0	0	2	3	3	4	3	3	3	2	3
<i>Schizoporella longirostris</i>	Slo	14	0	0	0	0	1	0	0	5	1	1	1	1	2	1	1
<i>Cladocora caespitosa</i>	Cca	2	10	1	3	1	0	1	1	2	3	2	2	2	2	3	2
<i>Balanophyllia europea</i>	Beu	0	1	0	2	0	3	7	14	2	2	2	2	2	3	3	3
<i>Cereus pedunculatus</i>	Cpe	2	13	5	0	0	0	0	0	2	4	3	1	2	1	1	2

determined by behavioural responses to small-scale patches of microhabitat and to different pattern of recruitment.

Due to the seasonality of Mediterranean shallow water communities (e.g., Boero 1994), with fluctuations in the presence and abundance of some species, the taxa identified as important could be less important in other seasons than late spring, when the survey was carried out. The available data on species composition are, however, assumed to reflect a set of environmental conditions that remain constant within a range of seasonal fluctuations.

Species richness differed among sectors, but only 6 taxa were important for sector differentiation. In this study, 4 taxa (*Calpensia nobilis*, filamentous brown algae, *Halimeda tuna*, *Peyssonellia squamaria*) had cover patterns that did not differ significantly in all sectors, their role of important species becoming evident only when considering their relative contribution to community structure. Only 1 taxon (encrusting calcified red algae) differentiated some sectors due to differences of cover, and another one (*Schizoporella longirostris*) by being absent in some sectors.

The *a priori* identification of important species is difficult and can usually be done only after the analysis of assemblage structure (Paine 1974, Underwood & Chapman 1998a).

However, the extraction of data on assemblage structure requires, besides quantitative estimates, taxonomic expertise sufficient to recognise conspicuous organisms underwater (Hiscock 1987), leading to species lists. This taxonomic effort in the field is compensated by no further identification work in the laboratory, apart from the examination of some voucher

specimens in the case of difficult species. Obviously, such species lists cannot be compared with those obtained by careful laboratory examination of destructive samples. However, more than 100 species recorded with such a simple and low-cost sampling effort can be considered quite a high number, sufficient to provide a quick and rough estimate of biodiversity over a large geographic area. Cryptic species and epiphytes are obviously lacking, but, on the other hand, many thin encrusting species, easily recognised and quantified visually, are difficult to collect efficiently by scraping the rock (Morri et al. 1999).

The multivariate approach showed less dissimilarity among sites within each sector than the average dissimilarity between each sector and all the remaining ones. However, sites within sectors were considerably different from each other, in spite of having been chosen at random to represent, in the same habitat, an assemblage that is supposed to be the same within each sector. This is in agreement with the high variability at site level recorded at other locations by Archambault & Bourget (1996) and Underwood & Chapman (1996, 1998a). As a consequence, replicate samples at different spatial scales are essential in any attempt to compare stretches of coast (Hurlbert 1984, Underwood & Denley 1984). A well-structured hierarchical design of sampling allows simultaneous assessment of pattern at multiple, overlapping scales (Underwood & Chapman 1998a).

On subtidal hard substrates, small-scale variability is commonly associated with developing assemblages (Glasby 1998), which seems consistent with the idea that communities in these sites consisted of patches at different developmental stages. In the present study a

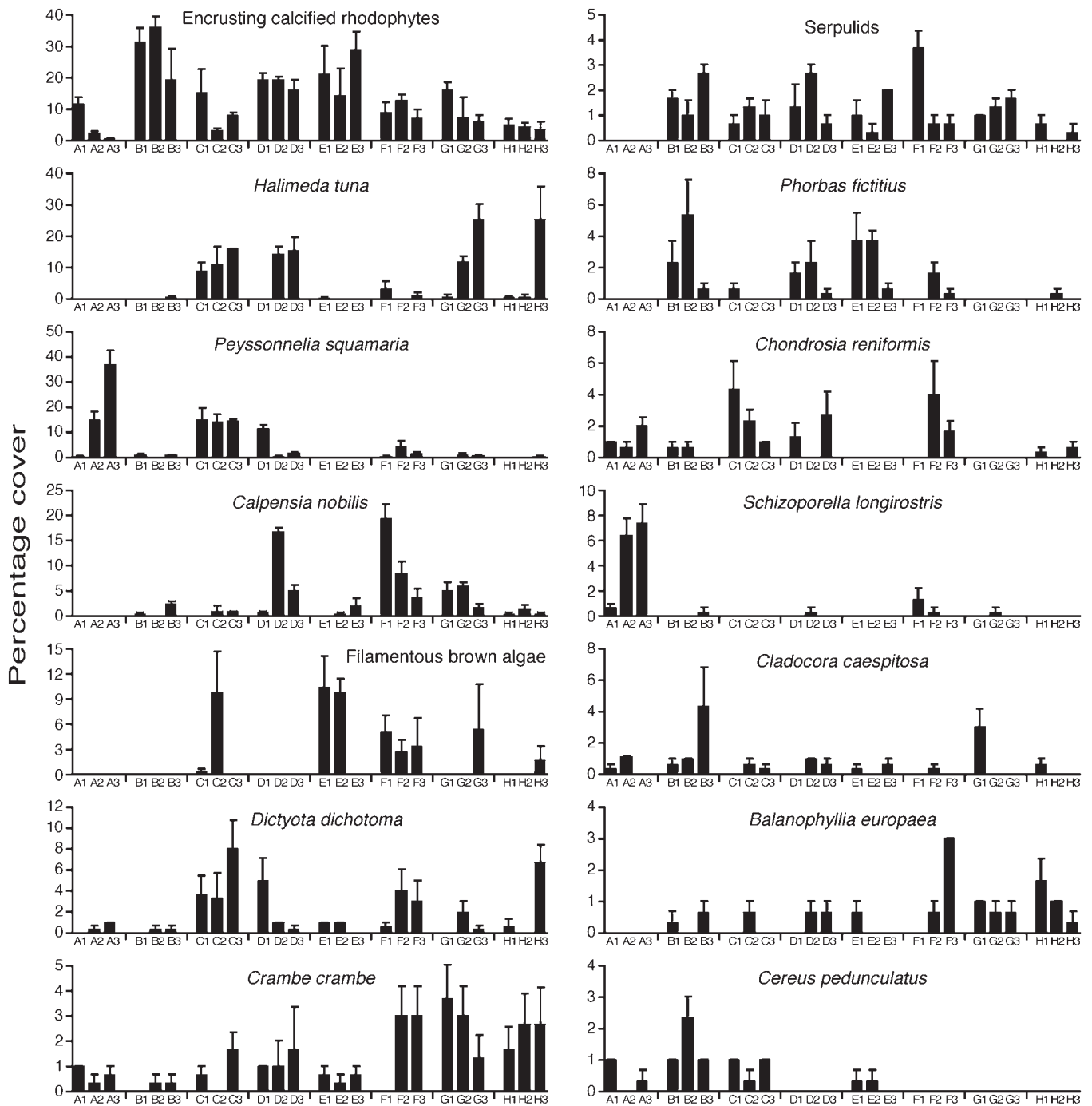


Fig. 7. Spatial distribution of percentage cover (mean \pm SE, $n = 3$) of taxa identified as important (see Table 4) in contributing to similarity within sites and/or dissimilarity among sectors

considerable variability among quadrats (expressed as the average value of similarity) was observed at most sites. The distribution pattern of assemblage similarity within sites was not significantly different among sectors, indicating that patchiness was homogeneously distributed throughout the whole region.

It is obviously not possible to explain all the ecological mechanisms accounting for the observed small-scale patchiness. Such processes include variation in settlement and recruitment, biotic interactions, and heterogeneity in the physical features of the habitat. It is, however, likely that disturbance contributes to cre-

Table 5. Results of ANOVAs testing for spatial differences in the percentage cover of 'important' taxa (ns: not significant; *p < 0.05; **p < 0.01; ***p < 0.001). The names of each taxon are coded as in Table 4.

Source of variation	df	Ecr		Htu		Psq		Cno		Fib		Ddi		Ccr	
		MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Sectors, S	7	675.68	7.67 ***	291.65	1.75 ns	428.37	3.04 ns	136.02	2.56 ns	52.03	1.84 ns	23.11	1.97 ns	7.48	3.43 *
Sl(S)	16	88.08	1.51 ns	166.82	6.72 **	141.01	12.52 **	53.15	15.75 ***	28.28	2.55 *	11.75	2.84 **	2.18	1.09 ns
Residual	48	58.49		24.82		11.26		3.38		11.11		4.14		2.00	
Cochran test (C)		C = 0.20		C = 0.25		C = 0.25		C = 0.27		C = 0.28		C = 0.21		C = 0.17	
		ns		p < 0.05		p < 0.05		p < 0.05		p < 0.05		ns		ns	
Source of variation	df	Ser		Pfi		Cre		Slo		Cca		Beu		Cpe	
		MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Sectors, S	7	3.66	1.69 ns	12.39	3.12 ns	7.87	2.24 ns	24.87	4.87 **	3.41	1.12 ns	1.64	1.25 ns	2.44	6.27 *
Sl(S)	16	2.17	4.73 ***	3.97	2.36 **	3.51	2.32 *	5.11	7.96 ***	3.04	2.99 *	1.32	6.79 ***	0.39	3.50 **
Residual	48	0.46		1.68		1.51		0.64		1.02		0.19		0.11	
Cochran test (C)		C = 0.21		C = 0.28		C = 0.25		C = 0.27		C = 0.26		C = 0.28		C = 0.25	
		ns		p < 0.05		p < 0.05		p < 0.05		p < 0.05		p < 0.05		p < 0.05	

ate patchiness at a small scale. Caswell & Cohen (1991) hypothesised that disturbance induces higher variability in communities. Warwick & Clarke (1993) recorded increased variability among replicate samples from several different marine communities exposed to distinct disturbances, thus providing support to the hypothesis and suggesting it may represent a general rule (but see also Chapman et al. 1995 for different findings). In the present case, the relationship between small-scale variability of community structure and damage caused by date mussel fisheries resulted in a curve (Fig. 6) similar to the predicted relationship between diversity and disturbance from the intermediate disturbance hypothesis (Connell 1978). Both sites with no disturbance and highly disturbed ones, in fact, were characterised by a lower level of 'patchiness' than sites with an intermediate level of disturbance. Under conditions of no disturbance, variability of the assemblage among replicate quadrats reflects a natural homogeneity of epibenthic assemblages at a small scale. When disturbance is very high, damage is uniformly distributed, so that all replicate quadrats represent a homogeneously degraded area. Community structure was more variable, at a small scale, when disturbance was intermediate (with D_v values comprised between 0.2 and 0.6). Date mussel fisheries, in this case, produce a mosaic of different community structures, leading to patchiness. At intermediate levels of disturbance, variability might be due to similar damage but of different age (replicate quadrats represented assemblages at different stages of recolonisation) or to the presence of damaged patches of similar age but of different area. As a consequence, also for subtidal epibenthic assemblages (at least at the considered depth, coinciding with the range of action of date mussel fishermen), intermediate levels of disturbance are effective in increasing variability at a small scale.

Our results, then, link Connell's (1978) hypothesis to the model of Warwick & Clarke (1993). It is reasonable to predict that under conditions of very high disturbance even the variability of the benthic communities analysed by Warwick & Clarke (1993) would have been very low, due to the almost complete eradication of living forms. This, in fact, was the case for the complete desertification of the Apulian subtidal rocky substrates due to the high impact of date mussel fisheries.

Human impact on target species and/or benthic communities has been widely studied (Moreno et al. 1984, Duran & Castilla 1989, McClanahan 1989, Castilla 1999, Lasiak 1999). As stressed in the introduction, however, no other form of human predation has a comparable impact to that of date mussel fisheries in terms of habitat destruction. Fanelli et al. (1994) showed that the damage due to date mussel fisheries was spreading from overexploited areas to underexploited ones. Five

years after those studies, date mussel fisheries did not show any sign of diminution in the whole considered area, in particular in Sector H, where disturbance levels were extremely high. During the 1997 survey, in spite of legislation prohibiting date mussel fisheries, we saw fishermen in action at 3 sites.

Disturbance acting at such a wide scale on the relative abundance of habitat types might have a strong impact on biodiversity. Danielson (1991) remarked that, even when the relative abundance of habitats does not change, variations in their spatial distribution could alter species interactions.

Strong action against this devastating form of human predation is urgently needed, especially aimed to convince consumers that the demand for date mussels is ecologically incorrect. The recent institution of Marine Protected Areas along the coast of Apulia will hopefully lead to habitat restoration and to the perception of the value of environmental integrity.

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LITERATURE CITED

- Airoldi L (1998) Roles of disturbance, sediment stress, and substratum retention on spatial dominance in algal turf. *Ecology* 79:2759–2770
- Archambault P, Bourget E (1996) Scales of coastal heterogeneity and benthic intertidal species richness, diversity and abundance. *Mar Ecol Prog Ser* 136:111–121
- Barry JP, Dayton PK (1991) Physical heterogeneity and the organization of marine communities. In: Kolasa J, Pickett STA (eds) *Ecological heterogeneity*. Springer Verlag, New York, p 270–320
- Bedulli D, Bianchi CN, Zurlini G, Morri C (1986) Caratterizzazione biocenotica e strutturale del macrobenthos delle coste pugliesi. In: Viel M, Zurlini G (eds) *Indagine ambientale del sistema marino costiero della regione Puglia*. ENEA, Roma, p 193–202
- Benedetti-Cecchi L, Menconi M, Cinelli F (1999) Pre-emption of the substratum and the maintenance of spatial pattern on a rocky shore in the northwest Mediterranean. *Mar Ecol Prog Ser* 181:13–23
- Benedetti-Cecchi L, Bulleri F, Cinelli F (2000) The interplay of physical and biological factors in maintaining mid-shore and low-shore assemblages on rocky coasts in the northwest Mediterranean. *Oecologia* 123:406–417
- Boero F (1994) Fluctuations and variations in coastal marine environments. *PSZN I: Mar Ecol* 15:3–25
- Boero F (1999) Macroecology returns. *J Evol Biol* 12:999–1001
- Bray JR, Curtis JT (1957) An ordination of the upland forest communities of Southern Wisconsin. *Ecol Monogr* 27:325–349
- Brown JH (1995) *Macroecology*. University of Chicago Press, Chicago
- Butler AJ, Chesson PL (1990) Ecology of sessile animals on sublittoral hard substrata: the need to measure variation. *Aust J Ecol* 15:521–531
- Carlile DW, Skalski JR, Batker JE, Thomas JM, Cullinan VI (1989) Determination of ecological scale. *Landscape Ecol* 2:203–213
- Castilla JC (1999) Coastal marine communities: trends and perspectives from human-exclusion experiments. *Trends Ecol Evol* 14:280–283
- Caswell H, Cohen JE (1991) Communities in patchy environments: a model of disturbance, competition, and heterogeneity. In: Kolasa J, Pickett STA (eds) *Ecological heterogeneity*. Springer-Verlag, New York, p 97–122
- Chapman MG (1994) Small-scale patterns of distribution and size-structure of the intertidal littorinid, *Littorina unifasciata* (Gastropoda: Littorinidae), in New South Wales. *Aust J Mar Freshw Res* 45:635–642
- Chapman MG, Underwood AJ, Skilleter GA (1995) Variability at different spatial scales between a subtidal assemblage exposed to the discharge of sewage and two control assemblages. *J Exp Mar Biol Ecol* 189:103–122
- Clarke KR (1993) Non parametric multivariate analyses of changes in community structure. *Aust J Ecol* 18:117–143
- Cocito S, Bianchi CN, Degl'Innocenti F, Forti S, Morri C, Sgorbini S, Zattera A (1991) Esempio di utilizzo di descrittori ambientali nell'analisi ecologica del paesaggio sommerso marino costiero. In: Farina A (ed) *L'ecologia dell'eterogeneità*. Zara, Parma, p 65–68
- Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310
- Connell JH, Sousa WP (1983) On the evidence needed to judge ecological stability or persistence. *Am Nat* 121:789–824
- Connolly SR, Roughgarden J (1999) Theory of marine communities: competition, predation, and recruitment-dependent interaction strength. *Ecol Monogr* 69:277–296
- Cornell HV, Karlson RH (1996) Species richness of reef-building corals determined by local and regional processes. *J Anim Ecol* 65:233–241
- Damiani V, Bianchi CN, Ferretti O, Bedulli D, Morri C, Viel M, Zurlini G (1988) Risultati su una ricerca ecologica sul sistema marino costiero pugliese. *Thal Salentina* 18:153–169
- Danielson BJ (1991) Communities in a landscape: the influence of habitat heterogeneity on the interactions between species. *Am Nat* 138:1105–1120
- Dayton PK, Thrush SF, Agardy TM, Hofman RJ (1995) Environmental effects of marine fishing. *Aquat Conserv Mar Freshw Ecosyst* 5:205–232
- Dethier MN, Graham ES, Cohen S, Tear LM (1993) Visual versus random-point percent cover estimations: 'objective' is not always better. *Mar Ecol Prog Ser* 96:93–100
- Dunson WA, Travis J (1991) The role of abiotic factors in community organization. *Am Nat* 138:1066–1091
- Duran LR, Castilla JC (1989) Variation and persistence of the middle rocky intertidal community of central Chile, with and without harvesting. *Mar Biol* 103:555–562
- Fanelli G, Piraino S, Belmonte G, Geraci S, Boero F (1994) Human predation along Apulian rocky coasts (SE Italy): desertification caused by *Lithophaga lithophaga* (Mollusca) fisheries. *Mar Ecol Prog Ser* 110:1–8

- Farina A (1998) Principles and methods in landscape ecology. Chapman and Hall, London
- Forman RTT, Godron M (1986) Landscape ecology. Wiley and Sons, New York
- Garrabou J, Riera J, Zabala M (1998a) Landscape pattern indices applied to Mediterranean subtidal rocky benthic communities. *Landscape Ecol* 13:225–247
- Garrabou J, Sala E, Arcas A, Zabala M (1998b) The impact of diving on rocky sublittoral communities: a case study of a bryozoan population. *Conserv Biol* 12:302–312
- Glasby TM (1998) Estimating spatial variability in developing assemblages of epibiota on subtidal hard substrata. *Mar Freshw Res* 49:429–437
- Glasby TM (1999) Differences between subtidal epibiota on pier pilings and rocky reefs at marinas in Sydney, Australia. *Estuar Coast Mar Sci* 48:281–290
- Guichard F, Bourget E (1998) Topographic heterogeneity, hydrodynamics, and benthic community structure: a scale-dependent cascade. *Mar Ecol Prog Ser* 171:59–70
- Hall SJ (1999) The effects of fishing on marine ecosystems and communities. Blackwell Science, Oxford
- Hewitt JE, Trush SF, Cummings VJ, Turner SJ (1998) The effect of changing sampling scales on our ability to detect effects of large-scale processes on communities. *J Exp Mar Biol Ecol* 227:251–264
- Hiscock K (1987) Subtidal rock and shallow sediments using diving. In: Baker JM, Wolf WJ (eds) Biological surveys of estuarine and coasts. Cambridge University Press, Cambridge, p 198–237
- Hughes TP, Baird AH, Dinsdale EA, Moltschaniwskij NA, Pratchett MS, Tanner JE, Willis BL (1999) Patterns of recruitment and abundance of corals along the Great Barrier Reef. *Nature* 397:59–63
- Hurlbert SJ (1984) Pseudoreplication and the design of ecological field experiments. *Ecol Monogr* 54:187–211
- Kennelly SJ, Underwood AJ (1993) Geographic consistencies of effects of experimental physical disturbance on understory species in sublittoral kelp forests in central New South Wales. *J Exp Mar Biol Ecol* 168:35–58
- Lasiak T (1999) The putative impact of exploitation on rocky infratidal macrofaunal assemblage: a multiple-area comparison. *J Mar Biol Assoc UK* 79:23–34
- Levin SA (1992) The problem of pattern and scale in ecology. *Ecology* 73:1943–1967
- Maurer BA (1999) Untangling ecological complexity. University of Chicago Press, Chicago
- McClanahan TR (1989) Kenyan coral reef-associated gastropod fauna: a comparison between protected and unprotected reefs. *Mar Ecol Prog Ser* 53:11–20
- Moreno CA, Sutherland JP, Jara HF (1984) Man as a predator in the intertidal zone of southern Chile. *Oikos* 42:155–160
- Morri C, Bianchi CN, Cocito S, Peirano A, De Biasi AM, Aliani S, Pansini M, Boyer M, Ferdeghini F, Pestarino M, Dando P (1999) Biodiversity of marine sessile epifauna at an Aegean island subject to hydrothermal activity: Milos, Eastern Mediterranean Sea. *Mar Biol* 135:729–739
- Naylor E (1995) Marine biology. In: Encyclopaedia Britannica Yearbook 1995. Encyclopaedia Britannica Inc, London, p 212
- Paine RT (1974) Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* 15:93–120
- Paine RT, Castilla JC, Cancino J (1985) Perturbation and recovery patterns of starfish-dominated assemblages in Chile, New Zealand and Washington State. *Am Nat* 125:679–691
- Pères JM (1982) Major benthic assemblages. In: Kinne O (ed) Marine ecology, Vol 5. J Wiley and Sons, London, p 373–508
- Peterson DL, Parker VT (eds) (1998) Ecological scale: theory and applications. Columbia University Press, New York
- Riedl R (1971) Water movement: animals. In: Kinne O (ed) Marine ecology, Vol 1. J Wiley and Sons, London, p 1123–1156
- Roberts DE (1996) Patterns in subtidal marine assemblages associated with a deep-water sewage outfall. *Mar Freshw Res* 47:1–9
- Russo GF, Cicogna F (1992) Il dattero di mare, *Lithophaga lithophaga* e gli effetti distruttivi della sua pesca sull'ambiente marino costiero: problemi e prospettive. *Boll Mus Ist Biol Univ Genova* 56/57:165–194
- Smith F, Witman JD (1999) Species diversity in subtidal landscapes: maintenance by physical processes and larval recruitment. *Ecology* 80:51–69
- Thompson RC, Wilson BJ, Tobin ML, Hill AS, Hawkins SJ (1996) Biologically generated habitat provision and diversity of rocky shore organisms at a hierarchy of spatial scales. *J Exp Mar Biol Ecol* 202:73–84
- Tilman D, Kareiva P (1997) Spatial ecology: the role of space in population dynamics and interspecific interactions. Princeton University Press, Princeton, NJ
- Underwood AJ (1997) Experiments in ecology: their logical design and interpretation using analysis of variances. Cambridge University Press, Cambridge
- Underwood AJ, Chapman MG (1996) Scales of spatial patterns of distribution of intertidal invertebrates. *Oecologia* 107:212–224
- Underwood AJ, Chapman MG (1998a) Spatial analyses of intertidal assemblages on sheltered rocky shores. *Aust J Ecol* 23:138–157
- Underwood AJ, Chapman MG (1998b) Variation in algal assemblages on wave-exposed rocky shores in New South Wales. *Mar Freshw Res* 49:241–254
- Underwood AJ, Denley EJ (1984) Paradigms, explanations and generalizations in models for the structure of intertidal communities on rocky shores. In: Strong DR, Simberloff D, Abele G, Thistle AB (eds) Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, NJ, p 151–180
- Warwick RM, Clarke KR (1993) Increased variability as a symptom of stress in marine communities. *J Exp Mar Biol Ecol* 172:215–226

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