Patterns of distribution of marine assemblages from rocky shores: evidence of relevant scales of variation

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ABSTRACT: Increasing evidence indicates that spatial and temporal patterns in ecological systems are not independent of the scale of measurement. In this study we used a hierarchical sampling design to examine spatial patterns in assemblages of algae and invertebrates in midshore and low-shore habitats of rocky coasts in the Mediterranean Sea, increasing the range of scales usually covered by this type of study in marine habitats. To put our results in a broader context, we also conducted a review of the literature, targeting studies that explicitly investigated spatial patterns with hierarchical designs. We addressed 2 main questions: (1) To what extent does small-scale variability contribute to large-scale patterns of variation? (2) Is there a pattern of variability that can be generalised across species and habitats? The review of the literature indicated that hierarchical analyses of spatial pattern have been limited to a narrow range of habitats and taxa and that very few studies have addressed regional scales of variation (1000s of kilometers). The available data, however, did identify a general pattern: variability was larger at small spatial scales (meters) in almost all habitats, whereas variation over larger spatial scales (10s to 100s of kilometers) depended on the specific habitat and taxa examined. In our case study, we obtained measures of spatial variability through the use of 2 alternative methods: hierarchical nested design and independent estimate of spatial variance between pairs of quadrats. Both approaches provided further support to the patterns displayed by the analysis of the literature. Most response variables exhibited large variation over small spatial scales, while the significance of mid- to large-scale variability differed between midshore and lowshore habitats and among taxa. Although a proper understanding of large-scale patterns will require additional comparisons across wide geographical areas, small-scale variability emerges as a general property of benthic assemblages in marine coastal habitats. We suggest that this pattern is common to a wide range of natural systems where assemblages are influenced by complex sets of physical and biological processes like those operating in the marine environment.

KEY WORDS: Spatial scale · Patchiness · Hierarchical ANOVA · Spatial variance · Rocky shores · Algae · Invertebrates

INTRODUCTION

The complexity of many ecological systems, underlying physical and biological heterogeneity at different spatial scales, is influencing the way ecologists view populations, communities and ecosystems (Holling 1992, Levin 1992). The appreciation of scale-dependent patterns is not a novelty; what is innovative is the recent expanded application of the concept in the design and interpretation of surveys, comparative studies and controlled experiments (Schneider 1994, Brown 1995, Maurer 1999). In terrestrial systems, the dependence of spatial patterns at different scales was first investigated in agricultural experiments (Mercer & Hall 1911). Different disciplines (from landscape ecology to geography) have contributed to generate new understanding of scale-dependent patterns and processes in physical and biological variables (Dungan et

al. 2002). The development of novel technical tools enabling the analysis of spatial patterns of populations over very small (~10^{-3} m) to very large (~10^{5} m) spatial scales and the refinement of statistical techniques for the analysis of such data have enhanced researchers' capacity to investigate a broad range of natural phenomena (Perry et al. 2002).

The analysis of spatial patterns of biodiversity in coastal marine systems has received wide attention, but the small size and cryptic nature of many marine organisms has prevented the broad use of recent technological innovations (e.g. remote sensing) in large-scale sampling. This has constrained the range of scales addressed by marine studies, which is usually smaller than that addressed by the terrestrial counterparts (but see Connolly & Roughgarden 1998, Broitman et al. 2001). Analyses in marine coastal systems have, however, highlighted common patterns of small- (10s to 100s of centimeters) to middle-scale (10s to 100s of meters) variation in the distribution and abundance of populations across a wide range of habitats and organisms (Foster 1990, Underwood & Chapman 1996, Menconi et al. 1999, Underwood et al. 2000, Benedetti-Cecchi 2001a, Kelaher et al. 2001, Olabarria & Chapman 2001). The general picture emerging from these studies is that small-scale processes are at least as important as large-scale processes in generating patterns in benthic assemblages and that small-scale spatial variance should not be considered simply as a statistical nuisance (Thrush et al. 1994, Horne & Schneider 1995, Coleman 2002).

Some evidence supports the view that local processes may scale up to generate large-scale patterns, suggesting that detailed studies at local scales are important to understand variation at the regional scale (Thrush et al. 1997a,b, Wootton 2001, Irving et al. 2004). Changes in small-scale spatial patterns are also used to assess potential symptoms of stress in marine assemblages (Warwick & Clarke 1993, Chapman et al. 1995, Fraschetti et al. 2001, Terlizzi et al. 2002) and recent advancements in statistical analysis allow a better quantification of small-scale patchiness, both in the univariate and multivariate contexts (Underwood & Chapman 1996, 1998a,b, Legendre & Anderson 1999, Terlizzi et al. 2005).

Although coastal habitats, such as intertidal and shallow subtidal environments, have proved to be tractable systems for analyses of spatial patterns in populations and assemblages (Archambault & Bourget 1996, Underwood & Chapman 1998a,b, Benedetti-Cecchi 2001a, Menge & Branch 2001, Fowler-Walker & Connell 2002, Fraschetti et al. 2002, Thompson et al. 2002), most studies have focused on a narrow range of spatial scales in a limited number of habitats (see 'Results: Review of the literature').

Investigating the influence of regional processes on populations and assemblages and determining the extent to which small-scale processes can be generalised, does require large-scale investigations (Lawton 1996). Few studies, however, have examined spatial variability over large scales (1000s of kilometers) in marine organisms (but see Åberg & Pavia 1997, Jenkins et al. 2000, 2001, Fowler-Walker & Connell 2002, Irving et al. 2004, Kelaher et al. 2004). The results of these investigations are somewhat contrasting, revealing little to no variability over regional scales in some instances and large variability in others. The extent to which the amount of small-scale variability compares to large-scale variation remains largely unexplored.

We address these issues in 2 ways: (1) through a review of the literature on the analysis of spatial patterns in marine habitats to document major achievements and possible gaps of knowledge on this topic, and (2) with a detailed study on spatial patterns in assemblages of midshore and lowshore habitats of rocky coasts in the Mediterranean. This analysis included 4 spatial scales, ranging from quadrats 10s of centimeters apart up to the regional scale, covering a spatial extent of more than 1000 km. We used a nested sampling design to test the null hypothesis that spatial pattern is invariant to scale in both habitats. Rejection of this hypothesis would lead to the identification of 1 or more relevant scales of spatial variation, providing clues on possible important processes for these assemblages.

Nested sampling designs in association with hierarchical analysis of variance are a powerful tool to investigate spatial (or temporal) patterns across scales. This approach, however, is not completely free of problems, as discussed in the recent literature (Palmer 1988, Rossi et al. 1992, Underwood & Chapman 1996, 1998a, Benedetti-Cecchi 2001a). A main issue in applying a hierarchical analysis of variance to a nested design is that intensity of sampling and therefore statistical power increases lower in the hierarchy. This prevents a direct comparison of the magnitude of variability at different scales (see Underwood & Petraitis 1993, Underwood & Chapman 1998a, Benedetti-Cecchi 2001a for further details).

To address these issues, spatial patterns in populations and assemblages were also compared using variances (or their multivariate analogues) between pairs of replicate units so that intensity of sampling was constant across scales.

MATERIALS AND METHODS

Review of the literature. We reviewed 39 studies reporting on analysis of spatial patterns in marine coastal habitats. These studies were selected by using

the 'Science Citation Index Expanded Database' on a web research platform (ISI Web of Science). The research was restricted to papers in English published from 1990 to 2004 and explicitly referring to the terms 'scale(s)' and/or 'spatial' (in association with the terms 'heterogeneity', 'pattern[s]', 'variability', 'variation') in the title, keywords and/or abstract. A variety of approaches have been used to quantify spatial variability in populations and assemblages (Rossi et al. 1992). Herein, we devoted attention to papers that explicitly used hierarchical sampling designs.

The review focused on vagile and sessile invertebrates and macroalgae that are common in marine coastal habitats. The following data were extracted from each study and synthesised in a table: targeted habitats (e.g. intertidal, subtidal), geographical areas of investigation, response variables (e.g. percentage cover, number of individuals, structure of assemblage), statistical procedures utilised to examine spatial patterns (i.e. uni- or multivariate analyses), the range of scales included and the main results (i.e. the relevant scales of variation, if any).

Study region and sampling design. Sampling was conducted in 2 regions, the Apulian coast of Italy and the Ionian coast of Greece, in late June 2001 (Fig. 1). The 2 stretches of coast occupy opposite sides of the south Adriatic Sea and fall between latitudes 41° 57′ and 37° 55′ N, more than 1000 km apart. In each re-

Fig. 1. Coasts of Italy and Greece. 1 to 7: sampling locations in each region

gion, 7 wave-exposed locations, separated by 10s to 100s of kilometers, were selected at random from a set of possible locations, characterised by relatively pristine habitats and comparable in terms of type and slope of the substratum. Due to the morphology of the coastline, the distance between 2 locations within a region was occasionally larger than the distance between 2 locations of different regions (Fig. 1). At each location, 4 sites (separated by 100s to 1000s of meters) were selected by moving at random distances from a point along the coast designated as the starting point of the location. Distances were selected using tables of random digits. At each of the 56 sites, 2 habitats were sampled, 1 at midshore heights (0.2 to 0.4 m above mean-low-level-water) and the other at low-shore heights (–0.1 to 0.1 m across mean-low-level-water) of the coast, with five 20 × 20 cm random quadrats in each habitat.

The midshore habitat was largely dominated by herbivores (*Patella* spp.) and encrusting algae. The low-shore habitat was characterised by dense stands of the brown algae *Cystoseira* spp., which is a canopy-forming group of species. These 2 habitats were selected on the basis of their accessibility, allowing sampling across a vast area (1000 km). The 2 habitats also enabled analyses of spatial patterns in very different assemblages along the emersion gradient of the shore.

Sampling methods. The percentage cover of sessile organisms was estimated in each quadrat by visual inspection. This was achieved by dividing the quadrat into 25 subquadrats of 4 × 4 cm; the abundance of each taxon was then assessed by giving a score from 0 to 4 to each subquadrat and adding up these values over the 25 subquadrats. Final values were expressed as percentages (Meese & Tomich 1992, Dethier et al. 1993). The abundance of some mobile invertebrates and of sea anemones in each quadrat was assessed as counts. Quadrats in the low-shore habitat were sampled by assessing the cover of *Cystoseira* spp. initially and then by quantifying the abundance of understorey organisms after removing the canopy from the substratum. Small and fast-moving animals such as amphipods and polychaetes were not considered. Destructive samples were also collected to aid the identification of taxa in the laboratory. Specialists assisted in the taxonomic identification of organisms.

Statistical analyses. *Nested analyses:* Spatial patterns of total number of taxa, total cover as well as cover of particularly abundant taxa were examined by a 3-way nested analysis of variance (ANOVA), with site nested in location and location nested in region. All factors were random. Variance components were estimated for each source of variation in ANOVAs by equating observed and expected mean squares (Winer
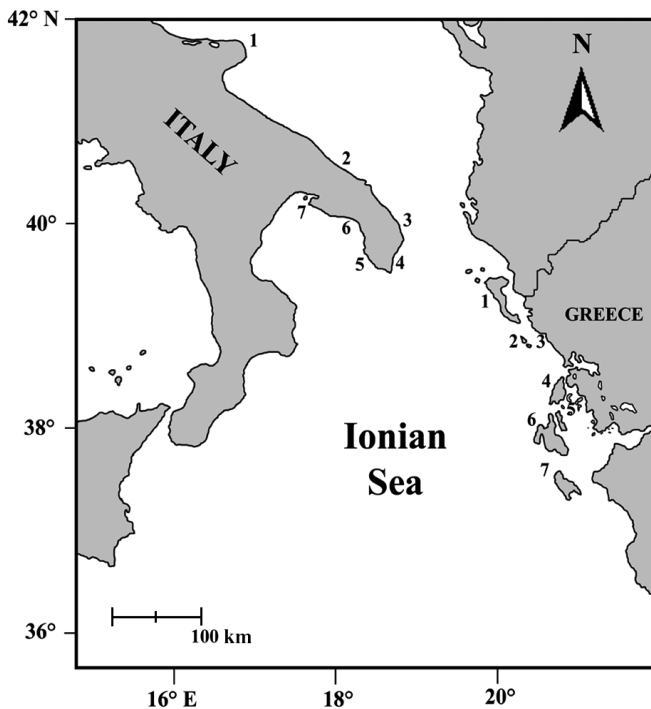
et al. 1991, Searle et al. 1992). Occasionally, negative estimates were obtained from the analysis. In these cases, negative values were set to zero, the corresponding factor removed from the model, and the estimates for the remaining factors re-calculated (Fletcher & Underwood 2002). All the analyses were done on untransformed data to provide variance components comparable across all data. Prior to analysis, Cochran's *C*-test was employed to assess homogeneity of variances. The more stringent criterion of $\alpha = 0.01$ was used to reject null hypotheses when variances were heterogeneous (Underwood 1997). When appropriate, Student-Newman-Keuls (SNK) tests were used for multiple comparisons of the means (at $\alpha = 0.05$). All the univariate analyses were done using the GMAV5 programme (University of Sydney, Australia).

Permutational multivariate analysis of variance (PERMANOVA; Anderson 2001a) was used to examine spatial variation in assemblages in the 2 habitats. The analyses were based on Bray-Curtis dissimilarities (Bray & Curtis 1957) on untransformed data (18 taxa for the midshore habitat and 54 for the lowshore habitat). Each term in the analyses was tested using 999 random permutations of the appropriate units (Anderson 2001b, Anderson & ter Braak 2003). The analyses were carried out using the FORTRAN program PERMANOVA (Anderson 2005). Since PERMANOVA allows the partitioning of the total variation in a way analogous to that performed by ANOVA, resulting mean squares were equated to the expected mean squares to estimate pseudo-variance components in the multivariate context (e.g. Benedetti-Cecchi 2001a).

For each habitat, non-metric multidimensional scaling ordinations (nMDS) (e.g. Kruskal & Wish 1978) were done on the basis of a Bray-Curtis dissimilarity matrix calculated from untransformed data. Ordinations were obtained by plotting the centroids of the 14 location cells to limit the number of observation points within plots. The arithmetic average across original variables does not correspond to the 'central location' in multivariate Bray-Curtis space (Anderson 2001a). Thus, to obtain centroids, principal coordinates were first calculated from the Bray-Curtis dissimilarity matrices among all pairs of the 280 quadrats and the arithmetic mean of these coordinates was then calculated. This was legitimate because the principal coordinate analysis places the observations into Euclidean space while preserving the Bray-Curtis distances among objects. The Euclidean distance between each pair of centroids was then calculated and used as the input distance matrix for the nMDS algorithm (e.g. Anderson 2001a).

As an example of small-scale variability in structure of assemblages in each habitat, data from a single location were analysed separately and the individual repli-

cates of the 4 sites of that location were plotted in an nMDS.

Pairwise comparisons: An alternative method (Underwood & Chapman 1998b) was used in order to maintain the intensity of sampling constant across scales and to obtain independent estimate of spatial variation at each scale. The data set was the same used in the previous analysis, besides the random selection of 6 out of the 7 locations available in each region to balance the data set. Data from midshore and lowshore habitats were analysed separately in this case also. The 5 quadrats available in each site and habitat were allocated randomly to 4 conditions that corresponded to contrasts of spatial variability at different scales. The first contrast used 2 of the 5 quadrats and provided a measure of spatial variability within the site. A third quadrat was contrasted with a quadrat of another site within the same location to yield a measure of variability between quadrats within a site plus the variability among sites. A fourth quadrat was contrasted with a quadrat from another site in a different location within the same region to measure the variability due to quadrats, sites and location. Finally, a fifth quadrat was paired with a quadrat from another region to measure the variability due to quadrats, sites, locations and regions. This procedure yielded 48 contrasts among quadrats within the same site and 24 contrasts at each of the other scales. To balance the data set, 24 of the 48 small-scale comparisons were selected randomly and used in analyses.

For univariate analyses, spatial variation was quantified as the variance between pairs of quadrats. For multivariate analyses, variability between pairs of quadrats was first measured as Bray-Curtis dissimilarities and then expressed as Euclidean distances following the procedure described for displaying the centroids of locations in nMDS plots (see previous subsection). Both univariate and multivariate measures of spatial variation were then compared across 4 scales (quadrat, quadrat + site, quadrat + site + location and quadrat + site + location + region) using a 1-way ANOVA with n = 24 observations in each level. SNK tests were used for multiple comparisons of the means (at $\alpha = 0.05$) allowing a test of the null hypothesis that spatial variation was invariant to scale.

RESULTS

Review of the literature

The analysis of the literature indicated that hierarchical analyses of spatial patterns in populations and assemblages were limited to a small number of habi-

tats and geographic areas, to few organisms and assemblages, and rarely covered spatial scales larger than 100s of kilometers. Furthermore, most studies took place in Australia, the North Atlantic region and the Mediterranean Sea. Few papers covered other geographical areas such as the Arctic (Lindegarth et al. 1995), Antarctic (Stark et al. 2003), South America (Uruguay, Giménez & Yannicelli 2000) or Central America (Belize; Farnsworth & Ellison 1996). The larger number of studies conducted in temperate areas was probably unrelated to particularly favorable environmental conditions for field work, since even tropical areas have not been investigated in detail for this specific topic (but see Farnsworth & Ellison 1996, Hughes et al. 1999). Moreover, most papers focused on rocky intertidal habitats. The distributional patterns of both populations and assemblages of intertidal soft bottoms have been explored to a smaller extent than those of hard bottoms (Lindegarth et al. 1995, Thrush et al. 1997a, Giménez & Yannicelli 2000) or Central America (Belize; Farnsworth & Ellison 1996). The larger number of studies conducted in temperate areas was probably unrelated to particularly favourable environmental conditions for field work, since even tropical areas have not been investigated in detail for this specific topic (but see Farnsworth & Ellison 1996, Hughes et al. 1999). Moreover, most papers focused on rocky intertidal habitats. The distributional patterns of both populations and assemblages of intertidal soft bottoms have been explored to a lesser extent than those of hard bottoms (Lindegarth et al. 1995, Thrush et al. 1997a, Giménez & Yannicelli 2000). The reason for this bias possibly resides in the long processing time of the large numbers of replicates that are required when a hierarchical sampling design is used. Of a total of 39 studies (Table 1), 18 explicitly recognised that rocky intertidal habitats are very convenient for fieldwork. The remaining papers dealt with the shallow subtidal (not deeper than 50 m), but the information was fragmented among shallow rocky bottoms (Kennelly & Underwood 1992, Fraschetti et al. 2001, Fowler-Walker & Connell 2002, Irving et al. 2004), bioconstructions (coralligenous formations, coral reefs) (Hughes et al. 1999, Ferdeghini et al. 2000), and soft bottoms (Morrisey et al. 1992, Li et al. 1997, Kendall & Widdicombe 1999, Stark et al. 2003, Zajac et al. 2003). Lagoons and estuaries, particularly relevant in terms of management of coastal habitats, have been largely neglected (but see Hodda 1990, Edgar & Barret 2002, Ysebaert & Herman 2002, De Biasi et al. 2003).

Only a few papers quantified the relative contribution of newly settled, juvenile, or adult organisms to the distributional patterns of the same species, also distinguishing brooders from free-spawners (Åberg & Pavia 1997, Hyder et al. 1998, Hughes et al. 1999,

Benedetti-Cecchi et al. 2000, Jenkins et al. 2000). There are 3 papers (Fowler-Walker & Connell 2002, Irving et al. 2004, Kelaher et al. 2004) that have examined spatial patterns over very broad spatial scales (1000s of kilometers), at the expense of detailed middle and/or small-scale analyses. Conversely, studies on intertidal gastropods have provided very detailed analyses of spatial patterns at scales ranging from centimeters to kilometers (the latter already being a 'large scale' for the organisms examined), but did not include regional comparisons (Chapman 1994a,b, 1995, 2002).

Only 1 paper could not identify significant variation at any of the scales investigated (Kendall & Widdicombe 1999), while other studies found significant variability at all the scales examined (e.g. Underwood & Chapman 1998b, Menconi et al. 1999, Coleman 2002, present study—see below).

Fowler-Walker & Connell (2002) and Irving et al. (2004) illustrated substantial variation in cover of benthic algae among sites kilometers apart, whereas variation was negligible at the scale of location (100s of kilometers) and at the regional scale (1000s of kilometers). Similarly, Åberg & Pavia (1997) showed differences in abundance of juvenile of the brown algae *Ascophyllum nodosum* at small scales, but not at the regional scale, while different results were obtained for adult individuals. Thus, repeatable patterns occurred over broad, but not over small spatial extents in these studies.

Significant variation in recruitment at all the spatial scales investigated (from 10s of meters to 100s–1000s of kilometers) was found by Jenkins et al. (2000) in a study relating settlement and recruitment of the barnacle *Semibalanus balanoides*. In contrast, a study examining a suite of response variables of the same species (from density to growth) indicated that most of the variability occurred among locations 100s to 1000s of kilometers apart (Jenkins et al. 2001). Significant differences were also found among sites 10s of meters apart for most variables, while variance components showed that differences between sampling units less than 0.5 m apart accounted for a low amount of the overall variability (Jenkins et al. 2001). Kelaher et al. (2004) found consistent differences across locations (1000s of kilometers) in the diversity and abundance of molluscs in coralline algal turf at the scale of site (10s of meters), suggesting possible generalities in the dominant processes that create such variation.

Nearly all populations and assemblages showed a patchy distribution at small spatial scales (the only exception being epiphytic macroalgae on *Posidonia coriacea*; Vanderklift & Lavery 2000). Apparently, this was the only scale at which a pattern common to most organisms emerged. Patterns became idiosyncratic

Table 1. Summary of studies on spatial patterns of distribution of populations and assemblages. Sources were selected on the basis of their explicit use of hierarchical nested designs. Authors' definitions of the relative importance of the different scales are reported. Low, High: nonsignificant effects that nevertheless were considered important by the author(s). *Spatial scale where significant variation occurred. An indication is given if significant effects were detected for few, some or most of analysed taxa or groups. NS: not significant. –: a spatial scale that was not included in the study. ANOVA: analysis of variance; ANCOVA: analysis of covariance; ANOSIM: analysis of similarities; CCA: canonical correspondence analysis; PERMANOVA: permutational multivariate analysis of variance; PCO: principal coordinate analyses

Habitat	Geographical area	Response variable	Statistical procedure	Scales included in the experimental designs								Source
				1000s of km	100s of km	10s of km	km	100s of m	10s of m	m	cm	
Intertidal hard substrata: *Nodilittorina piramidalis*	Australia	No. of individuals	ANOVA	–	–	–	*	*	–	*	*	Chapman (1994a)
Intertidal hard substrata: gastropods and 1 cirriped	Australia	No. of individuals	ANOVA/variance components	–	–	*(Some taxa)	*(Some taxa)	*(Some taxa)	*	*	*	Underwood & Chapman (1996)
Intertidal hard substrata: phytal ostracods of tidepools	Northeast coast of England	Total abundance	ANOVA	–	–	NS	–	NS	–	NS	–	Hull (1999)
		Abundance of most abundant taxa	ANOVA	–	–	*(Few taxa)	–	*(Most taxa)	–	*(Few taxa)	–	
		Total number of taxa	ANOVA	–	–	*	–	NS	–	NS	–	
Intertidal hard substrata (coralline turf): microgastropods	Australia	Abundance of most abundant taxa	ANOVA	–	–	–	–	*(Few taxa)	*(Few taxa)	*(Most taxa)	–	Olabarria & Chapman (2001)
Intertidal shores (sandy sediments): microgastropods		Abundance of most abundant taxa	ANOVA	–	–	–	–	*(Few taxa)	*(Few taxa)	*(Few taxa)	–	
Intertidal hard substrata: molluscs	North Atlantic	Abundance of most abundant taxa / Structure of the assemblage	ANOVA/variance components / ANOSIM	–	–	NS	*(Most taxa)	*(Few taxa)	–	NS	–	Johnson et al. (2001)
Intertidal hard substrata (coralline turf): molluscs	Australia Chile Ireland	Abundance of most abundant taxa	ANOVA	*	–	NS	–	–	*(Most taxa)	–	–	Kelaher et al. (2004)
Intertidal hard substrata: echinoderms-molluscs	Australia	No. of individuals	ANOVA/variance components	–	–	–	–	–	*(Some taxa)	High	–	Chapman (2002)
		Structure of the assemblage	PERMANOVA	–	–	–	–	–	*	High	–	
Intertidal hard substrata: *Semibalanus balanoides* recruits	North Atlantic	No. of individuals	ANOVA/variance components	–	*	–	*	–	*	High	–	Jenkins et al. (2000)[a]
Intertidal hard substrata: *Semibalanus balanoides* adults	North Atlantic	No. of individuals	ANOVA/variance components	–	–	NS	NS	*	–	NS	High	Hyder et al. (1998)
Intertidal hard substrata: *Semibalanus balanoides* adults	North Atlantic	No. of individuals	ANOVA/variance components	–	*	–	NS	–	*	Low	–	Jenkins et al. (2001)[a]
Intertidal hard substrata: *Chthamalus stellatus*	Northwest Mediterranean Sea	No. of individuals (recruits)	ANOVA/variance components	–	–	High	–	Low	–	High	–	Benedetti-Cecchi et al. (2000)
Intertidal hard substrata: mobile epifauna assemblage of seaweeds	North Atlantic	Structure of the assemblage	ANOSIM	*	–	–	–	–	–	–	–	Viejo & Aberg (2003)
Intertidal hard substrata: mobile epifauna single taxa of seaweeds	North Atlantic	No. of individuals of mesograzers	ANOVA	–	–	–	–	–	*(Most taxa)	*(Most taxa)	–	

[a] Jenkins et al. (2000, 2001) named the largest scale 100s of km, but both studies actually covered a spatial scale of 1000s of km and therefore were included in the biogeographical analyses

Table 1 (continued)

Habitat	Geographical area	Response variable	Statistical procedure	Scales included in the experimental designs								Source
				1000s of km	100s of km	10s of km	km	100s of m	10s of m	m	cm	
Intertidal hard substrata: macrorecruits and adults of the seeweed *Ascophyllum nodosum*	North Atlantic	No. of individuals (juveniles)	ANOVA / variance components	NS	–	–	NS	–	*	*	High	Aberg & Pavia (1997)
Intertidal hard substrata: algae and invertebrates	Canada	Total number of taxa	ANCOVA	–	–	–	NS	*	*	–	Low	Archambault & Bourget (1996)
		Abundance	ANOVA	–	–	–	NS	NS	–	–	*	
Intertidal hard substrata: algae and invertebrates	Australia	Structure of the assemblage	ANOSIM	–	–	–	*	–	*	*	–	Underwood & Chapman (1998b)
		Abundance of most abundant taxa	ANOVA	–	–	–	*	–	*	*	–	
Intertidal hard substrata: algae and invertebrates	Northwest Mediterranean Sea	Abundance of most abundant taxa	ANOVA	–	–	*	*	–	*	–	*	Menconi et al. (1999)
Intertidal hard substrata: algae and invertebrates	Northwest Mediterranean Sea	Abundance of most abundant taxa	ANOVA / PERMANOVA	–	*(Some taxa)	*(Some taxa)	–	NS	*(Some taxa)	*(Some taxa)	–	Benedetti-Cecchi (2001a)
Intertidal hard substrata: algal turf	Australia	Structure of the assemblage	ANOSIM	NS	–	*	–	–	*	–	High	Coleman (2002)
		Cover of most abundant taxa	ANOVA	–	–	*	–	–	*	–	High	
Shallow subtidal hard substrata: algal turf		Structure of the assemblage	ANOSIM	–	–	*	–	–	*	–	High	
		Cover of most abundant taxa	ANOVA	–	–	*	–	–	*	–	High	
Intertidal hard substrata: algae and invertebrates	Northwest Mediterranean Sea	Abundance of most abundant taxa	ANOVA / variance components	–	*(Some taxa)	*(Some taxa)	*(Most taxa)	–	–	–	–	Benedetti-Cecchi et al. (2003)
		Structure of the assemblage	ANOSIM	–	*	*	*	–	–	–	–	
Intertidal hard substrata: algae and invertebrates	Western Mediterranean Sea	Abundance of most abundant taxa / Structure of the assemblage	ANOVA / variance components	NS	–	*	*	–	–	High	–	Present study
Shallow subtidal hard substrata: algae and invertebrates		Abundance of most abundant taxa / Structure of the assemblage	ANOVA / PERMANOVA	*	*	*	*	–	–	High	–	
Epiphytic macroalgae on *Posidonia coriacea*	Australia	Presence/absence data	ANOSIM	–	–	–	High	–	–	–	*	Vanderklift & Lavery (2000)
Mangrove root epibiont communities	Belize	Structure of the assemblage	Jaccard's index / Kendall's coeff. / cluster analysis	–	–	–	*	*	*	NS	*	Farnsworth & Ellison (1996)
Corals: recruitment and abundance	Australia	Spawning adults	ANOVA / variance components	–	NS	NS	*	–	–	NS	–	Hughes et al. (1999)
		Brooding adults		–	*	NS	*	–	–	NS	–	
Subtidal hard substrata: kelp canopy-benthic associations	Australia	Abundance of most abundant taxa	ANOVA	–	*	–	*	–	*	*	–	Kennelly & Underwood (1992)
Subtidal hard substrata: bioconstructors	Western Mediterranean Sea	Abundance of most abundant taxa	ANOVA	–	–	–	*(Few taxa)	*(Few taxa)	*(Most taxa)	–	–	Ferdeghini et al. (2000)
		Total cover / cover of some taxa	ANOVA	–	*(Few taxa)	–	*(Most taxa)	–	–	–	–	
Subtidal hard substrata: sessile macrobenthos	Western Mediterranean Sea	Total number of taxa	ANOVA	–	*	*	*	–	–	–	–	Fraschetti et al. (2001)
		Structure of the assemblage	ANOSIM	–	*	*	*	–	–	High	–	

Table 1 (continued)

Habitat	Geographical area	Response variable	Statistical procedure	Scales included in the experimental designs								Source
				1000s of km	100s of km	10s of km	km	100s of m	10s of m	m	cm	
Subtidal hard substrata: kelp canopy-benthic associations	Australia	Structure of the assemblage	PERMANOVA	*	–	–	–	–	–	–	–	Fowler-Walker & Connell (2002)
	Australia	Cover and densities of groups of algae and grazers	ANOVA	*(Most taxa)	*(Few taxa)	–	*(Most taxa)	–	–	–	–	Irving et al. (2004)
Subtidal hard substrata: canopy-benthic associations	Australia New Zealand	Structure of the assemblage	PERMANOVA	*	*	–	*	–	–	–	–	
		Cover of morphological groups	ANOVA	*(Few taxa)	*(Most taxa)	–	*	–	–	–	–	
Intertidal sandy bays: infaunal bivalves	North Sea	Abundance of Cerastoderma edule	ANOVA / variance components	–	NS	NS	–	*	NS	High	–	Lindegarth et al. (1995)
		Abundance of Cerastoderma lamarcki	ANOVA / variance components	–	NS	*	–	*	NS	High	–	
Intertidal sandy beach: macrobenthos	Uruguay	No. of individuals	ANOVA	–	–	–	*(Some taxa)	*	*	–	–	Giménez & Yannicelli (2000)
Estuaries: macrobenthos	Tasmania	No. of taxa	ANOVA / variance components	–	High	Low	–	Low	–	High	–	Edgar & Barrett (2002)
		No. of individuals		–	Low	High	–	Low	–	High	–	
		Biomass		–	High	Low	–	Low	–	High	–	
		Productivity		–	High	Low	–	Low	–	High	–	
Estuaries: macrobenthos	The Netherlands	No. of individuals	ANOVA / variance components	–	–	NS	NS	*	–	–	–	Ysebaert & Herman (2002)
		Structure of the assemblage	CCA	–	–	High	NS	–	–	–	–	
Coastal lagoon: algae, phanerogams and invertebrates	Western Mediterranean Sea	Abundance of most abundant taxa	ANOVA	–	–	–	–	*	*	–	–	De Biasi et al. (2003)
		Structure of the assemblage	ANOSIM	–	–	–	–	*	*	–	–	
Subtidal macrobenthos	Australia	No. of taxa	ANOVA / variance components	–	–	NS	*	*	*	NS	–	Morrisey et al. (1992)
		No. of individuals		–	–	NS	NS	*	*	–	–	
Subtidal macrobenthos: a sandy mud	North Atlantic Sea	Structure of the assemblage	ANOSIM	–	–	–	–	*	NS	NS	–	Kendall & Widdicombe (1999)
Subtidal macrobenthos: a very fine sand		Structure of the assemblage		–	–	–	–	NS	NS	NS	–	
Subtidal macrobenthos	Antarctica	Abundance of most abundant taxa	ANOVA / variance components	–	–	–	*	*(Most taxa)	*	*	–	Stark et al. (2003)
Subtidal macrobenthos	North Atlantic Sea	Abundance of most abundant taxa	ANOVA / variance components	–	–	*(Few taxa)	*(Few taxa)	–	–	*(Most taxa)	–	Zajac et al. (2003)[b]
Estuaries: meiobenthos	Australia	Structure of the assemblage	Cluster and PCO	–	Low	–	–	–	High	–	High	Hodda (1990)
Subtidal meiobenthos	North Sea	Abundance of most abundant taxa	ANOVA	–	–	*	*	–	–	NS	High	Li et al. (1997)
Subtidal meiobenthos	White Sea	Abundance of most abundant taxa	ANOVA / variance components	–	–	–	–	–	High	High	Low (most taxa)	Azovsky et al. (2004)

[b]Scale order is of 2 to 3 km^2

both for modular and individual organisms when moving above the scale of meters (Farnsworth & Ellison 1996, Hyder et al. 1998, Hughes et al. 1999, Hull 1999, Jenkins et al. 2001, Olabarria & Chapman 2001).

Finally, very few studies examined simultaneously spatial and temporal variation, so that tests of space × time interactions are uncommon in the literature (Kennelly & Underwood 1992, Åberg & Pavia 1997, Underwood & Chapman 1998b, Menconi et al. 1999, Jenkins et al. 2000, Chapman 2002, Ysebaert & Herman 2002, De Biasi et al. 2003).

Present study

Midshore assemblage

Overall, 18 taxa were identified. Of these, 5 were identified to species. The most common organisms were cyanobacteria (*Rivularia* spp.), gastropods (the limpets *Patella rustica* Linné and *P. aspera* Röding, the littorinid snail *Melaraphe neritoides* [Linné]), barnacles (*Chthamalus stellatus* [Poli]) and encrusting calcified red algae (including *Lithophyllum* sp*.* and *Peyssonnelia* sp.).

Nested analyses: Results of ANOVAs of mean percentage cover and total number of taxa are summarised in Table 2. Both variables showed no significant differences at the scale of region and locations, but differed significantly at the scale of site. The estimate of residual variance was always larger than the variance components associated with larger spatial scales, indicating that variation among replicate units was important.

ANOVA was also performed to compare spatial variation across scales for the most abundant taxa. Table 3 summarises results for bacteria, encrusting calcified red algae (ECR), *Chthamalus stellatus* and *Patella* spp. All taxa differed significantly at the scale of site, whereas there were no differences among locations and between regions. Variance components exhibited the same pattern described above for the mean per-

Table 2. ANOVA testing for spatial differences in mean cover and mean number of taxa in the 2 habitats (***$p < 0.001$; *$p < 0.05$; ns: not significant) at scales of region, location and site. Estimates of variance components are included

Source	df	Cover			Number of taxa		
		MS	F	Variance component	MS	F	Variance component
Midshore assemblage							
Region = R	1	1939.89	0.66[ns]	0.00	19.56	5.20[ns]	0.54
Location(R) = L(R)	12	2951.71	1.78[ns]	60.95	3.76	0.85[ns]	0.00
Sites(L(R)) = S(L(R))	42	1654.80	7.76***	288.30	4.45	3.56***	0.61
Residual	224	213.32		213.32	1.25		1.25
Total	279						
Cochran's C-test		0.07[ns]				0.11*	
Transformation		None				None	
Lowshore assemblage							
Region = R	1	4690.41	2.31[ns]	19.01	18.51	0.31[ns]	0.00
Location(R) = L(R)	12	2029.35	3.53***	72.71	60.36	4.48***	2.18
Sites(L(R)) = S(L(R))	42	575.21	2.43***	67.64	13.49	2.82***	1.74
Residual	224	237.00		237.00	4.78		4.78
Total	279						
Cochran's C-test		0.07[ns]				0.06[ns]	
Transformation		None				None	

Table 3. ANOVA testing for spatial differences in mean percentage cover of abundant taxa in midshore habitat. ECR: encrusting calcified red algae. ***$p < 0.001$; ns: not significant

Source	Region = R			Location(R) = L(R)			Sites(L(R)) = S(L(R))			Residual
	MS	F	Variance component	MS	F	Variance component	MS	F	Variance component	
Bacteria[a]	0.80	0.02[ns]	0.00	44.16	1.55[ns]	0.79	28.41	2.00***	2.84	14.18
Chthamalus stellatus[a]	2206.41	2.13[ns]	8.36	1035.07	1.24[ns]	9.89	837.19	13.01***	154.56	64.35
Patella spp.[a]	304.51	1.07[ns]	0.13	285.60	1.80[ns]	6.35	158.43	4.60***	24.79	34.46
ECR	2123.00	4.78[ns]	11.99	443.95	1.84[ns]	6.92	305.60	2.95***	286.85	90.73
[a]Variances heterogeneous										

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centage cover and total number of taxa, except for *C. stellatus*, in which most of the variation was observed at the scale of site.

PERMANOVA provided evidence of 2 relevant scales of spatial variation: the scale of location and that of site (Table 4). No significant difference was found at the
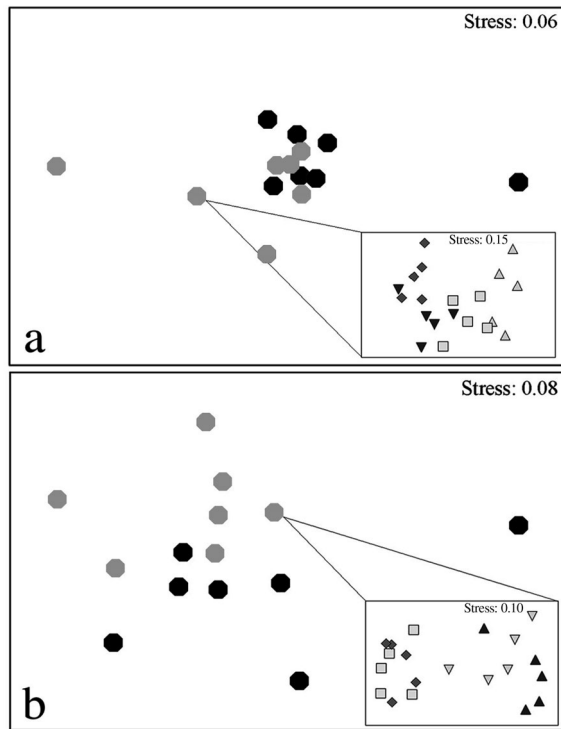
scale of region. Estimates of multivariate variation increased with decreasing spatial scale. Residual variation, indicating multivariate heterogeneity among quadrats, was much larger than variation at any other scale. There was a clear pattern of decreasing multivariate variation from small to large spatial scales (Table 4). Visual inspection of nMDS plots reflected the results of the PERMANOVA (Fig. 2a): the structure of the assemblage of the midshore habitat showed a negligible separation between the 2 regions. Most locations were intermingled and there was no evidence of regional variation. An illustrative example of patterns of variation at the level of individual sites within one of the seven locations is shown in Fig. 2a.

Pairwise comparisons: The analyses based on pairwise comparisons among sampling units indicated that most of the variation in univariate data was among quadrats, with no further contribution of variability added by larger scales (see results of SNK tests, Fig. 3). The only exception was represented by bacteria (Fig. 3), for which the analysis revealed significant differences among scales. Graphical inspection suggested that sites added a significant contribution of variance above that of quadrats, but the SNK test could not provide a clear alternative to the null hypothesis. The analysis of multivariate variation also provided evidence of largest variability at the scale of replicate quadrats (Fig. 4a).

Fig. 2. Non-metric multidimensional scaling ordinations (nMDS plots) on the basis of Bray-Curtis dissimilarity measure of (a) centroids of 14 location cells of midshore habitat and (b) centroids of 14 location cells of lowshore habitat. (●) 7 locations on the Ionian coast of Greece; (●) 7 locations on the Apulian coast of Italy. Insets: in each habitat, data from a single location were analysed separately and the individual replicates of the 4 sites of that location are also shown as subplots, in which symbols identify 5 replicate quadrats for each of the 4 sites

Lowshore assemblage

The canopy-forming species *Cystoseira amentacea* Bory var. *stricta* Montagne was dominant along the surveyed coast, but occasionally *C. compressa* (Esper) Gerloff & Nizamuddin and *C. barbatula* Kützing also occurred in samples. Overall, 54 taxa (16 identified to species) were counted in the assemblage under the canopy. They included *Corallina elongata* Ellis et Solander, *Valonia utricularis* (Roth) C. Agardh, and

Table 4. Results of PERMANOVAs testing for spatial differences in structure of assemblages at scales of region, location and site. Analyses based on Bray-Curtis dissimilarities from untransformed data. Each term was tested using 999 random permutations of appropriate units. Estimates of multivariate variation are given for each spatial scale. **p < 0.01; ***p < 0.001; ns: not significant

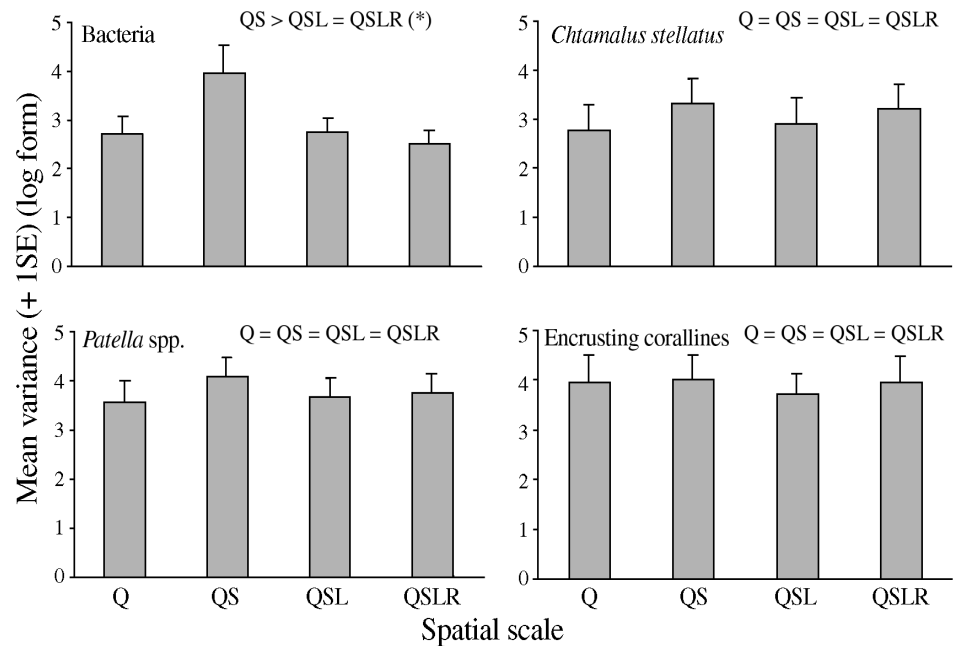| Source	df	Midshore assemblage			Lowshore assemblage		
		MS	F	Estimates of spatial variation	MS	F	Estimates of spatial variation
Region = R	1	15370.84	1.48[ns]	35.61	59925.99	2.76**	273.09
Location(R) = L(R)	12	10385.41	2.02***	261.88	21693.53	4.32***	833.59
Sites(L(R)) = S(L(R))	42	5147.74	3.53***	738.15	5021.73	2.91***	659.53
Residual	224	1456.97		1456.97	1724.10		1724.10
Total	279						
Transformation	None					None	

Fig. 3. Mean (+1 SE), n = 24) estimates of variance in abundance (log form) of algae and invertebrates at 4 spatial scales in the midshore habitat. Results of SNK tests comparing variances at different scales are included. Q: quadrat; QS: quadrat + site; QSL: quadrat + site + location; QSLR: quadrat + site + location + region. (*) The only interpretable result, as Q was not consistently ranked by SNK test
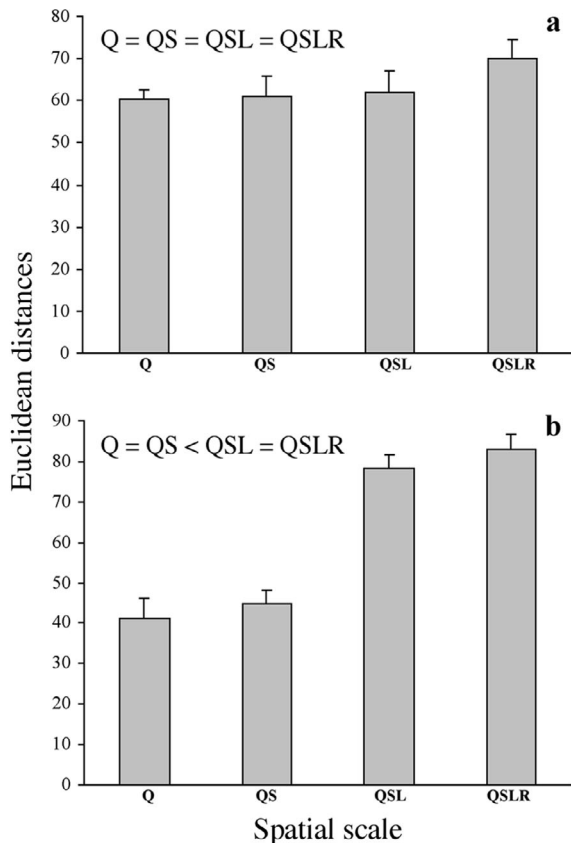

Fig. 4. Mean (+SE, n = 24) estimates of multivariate variation at 4 spatial scales. Data expressed as Euclidean distance between any pair of observations using principal coordinates. (a) midshore habitat; (b) lowshore habitat. Results of SNK tests comparing Euclidean distances at different scales are included; abbreviations as in Fig. 3

Halimeda tuna (Ellis et Solander) Lamouroux among the algae, and the sponge *Ircinia foetida* (Schmidt) and the ascidian *Diplosoma listerianum* (Milne-Edwards) among the invertebrates.

Nested analyses: Results of ANOVAs on mean percentage cover and number of taxa are summarised in Table 2. Both variables showed no significant differences at the scale of region, but differed significantly at the scale of location and site. Most variability occurred at the smallest spatial scale, among quadrats, as indicated by the large values of the residual mean squares.

Analysis of variance (Table 5) indicated that all the variables analysed did not differ at the scale of region. In particular, *Cystoseira amentacea*, *Corallina elongata*, the ascidian *Diplosoma listerianum*, articulated corallines and dark filamentous algae were characterised by significant differences in their cover at the scales of location and site. In contrast, ECR varied significantly only at the scale of location. Variance components at the scale of replicate quadrats, as indicated by residual mean squares, were always larger than those at the other scales irrespective of the taxon considered.

PERMANOVA provided evidence that the structure of understorey assemblages differed significantly at all scales considered in the study (Table 4). Estimates of multivariate variation increased with decreasing spatial scale, the largest variation occurring among replicate quadrats, as indicated by the residual mean square.

The nMDS plot (Fig. 2b) illustrates clearer differences between the 2 regions than those observed for the midshore assemblage (Fig. 2a). In addition, locations were widely scattered, providing evidence of

Table 5. ANOVA testing for spatial differences in mean percentage cover of abundant taxa in lowshore habitat. **p < 0.01; ***p < 0.001; ns: not significant. Variances were heterogeneous in all cases. Abbreviations as in Table 3

Source	Region = R			Location(R) = L(R)			Sites(L[R]) = S(L[R])			Residual
	MS	F	Variance component	MS	F	Variance component	MS	F	Variance component	
Cystoseira spp.	939.88	0.12[ns]	0.00	7355.04	5.84***	304.80	1259.02	3.41***	178.03	368.89
Hydroids	391.29	4.11[ns]	2.11	95.15	1.61[ns]	1.80	58.99	1.82**	5.31	32.43
Sea anemones	23.43	1.69[a]	0.07	13.89	1.46[ns]	0.21	9.51	3.66***	1.38	2.60
Didemnidae	1160.36	7.18[a]	7.13	161.57	2.56[a]	4.92	63.19	3.14***	8.62	20.10
Diplosoma listerianum	117.00	6.03[a]	0.70	19.39	3.06***	0.65	6.34	2.31***	0.73	2.74
Articulated corallines	284.01	0.51[ns]	0.00	536.93	2.30**	15.16	233.73	3.87***	34.66	60.41
Corallina elongata	5688.01	6.72[a]	34.58	846.18	3.26**	29.32	259.80	3.67***	37.79	70.87
Dark filamentous algae	78.23	0.59[ns]	0.00	127.60	3.08**	4.31	41.45	3.42***	5.86	12.13
ECR	393.65	2.75[ns]	1.79	142.92	2.84**	4.63	50.28	1.56[a]	3.62	32.19

[a]Term not significant at $\alpha = 0.01$; this conservative level of significance was adopted because variances were heterogeneous

important variation at the scale of kilometers. As for the midshore habitat, the nMDS in Fig. 2b shows in more detail an example of the spatial variability of the assemblage within one location, at the scale of site. Also in this case, patchiness at the scale of replicate quadrats was very large (Fig. 2b: inset).

Pairwise comparisons: The analysis of spatial variation based on pairwise comparisons highlighted the importance of small-scale variability, indicating more variation at the scale of quadrats compared to that occurring at any other scale in all taxa (SNK test, Fig. 5). The analysis of multivariate variation showed that locations added a significant contribution of variance above that of replicate quadrats (Fig. 4b).

DISCUSSION

Resolving the relative contribution of local versus regional processes may be key to understanding global patterns of species diversity (Huston 1999). Over very small spatial scales (centimeters to meters), experimental manipulations and descriptive studies have provided considerable insights into local ecological dynamics (Connolly & Roughgarden 1998). At larger scales (100s to 1000s of kilometers), traditional biogeographic studies provided perspectives on the processes influencing whole assemblages (Brown 1995, Maurer 1999, Broitman et al. 2001). Between local and biogeographic scales, however, there is a suite of processes that only recently has received proper attention, and information has yet to be integrated.

Our review of the literature highlighted a general theme: variability is large at small scales in almost all the habitats examined. Small-scale patchiness in the distribution of benthic organisms is repeatedly demonstrated, since nearly all populations and assemblages (even in soft sediments, usually considered as homogeneous habitats) show a patchy distribution for all the consid-

ered variables at the scale of centimeters. With very few exceptions (Farnsworth & Ellison 1996, Li et al. 1997, Hyder et al. 1998), small-scale patchiness is still common when scales increase from centimeters to meters. The significance of this large spatial variance at the small scale has been discussed in several papers and suggests that local biological interactions and small-scale physical processes are pervasive in marine systems (see Underwood & Petraitis 1993, Underwood 1996, Legendre et al. 1997, Benedetti-Cecchi et al. 2001a, Coleman 2002, for detailed discussions of the potential processes that may generate large spatial variance at a small scale), similar to the situation in terrestrial habitats (Picket & White 1985, Leponce et al. 2004).

Not all studies, however, concur that spatial variation decreases as the scale of measurement increases. Denny et al. (2004), for example, found that the variance of several physical and biological variables measured along a stretch of rocky coast in California increased with increasing spatial scale. Denny et al. (2004) suggested that the topography of the substratum may affect scaling relationships in intertidal habitats. In contrast to the studies included in our review of the literature, Denny et al. (2004) examined patterns of variability along continuous spatial scales and used spectral analyses to characterise these patterns. Thus, it is possible that differences in sampling design (continuous versus discrete spatial scales) and method of analysis (spectral analyses versus analysis of variance) are responsible for the discrepancy between the results reported by Denny et al. (2004) and those of the studies reviewed by us.

Methodological issues, however, may not be the only cause of this discrepancy. Johnson et al. (2001), using a hierarchical sampling design to investigate spatial variation in density of intertidal molluscs on rocky shores of the Isle of Man, showed that life history may affect the importance of scale. Species with a larval dispersal stage displayed more variation among shores
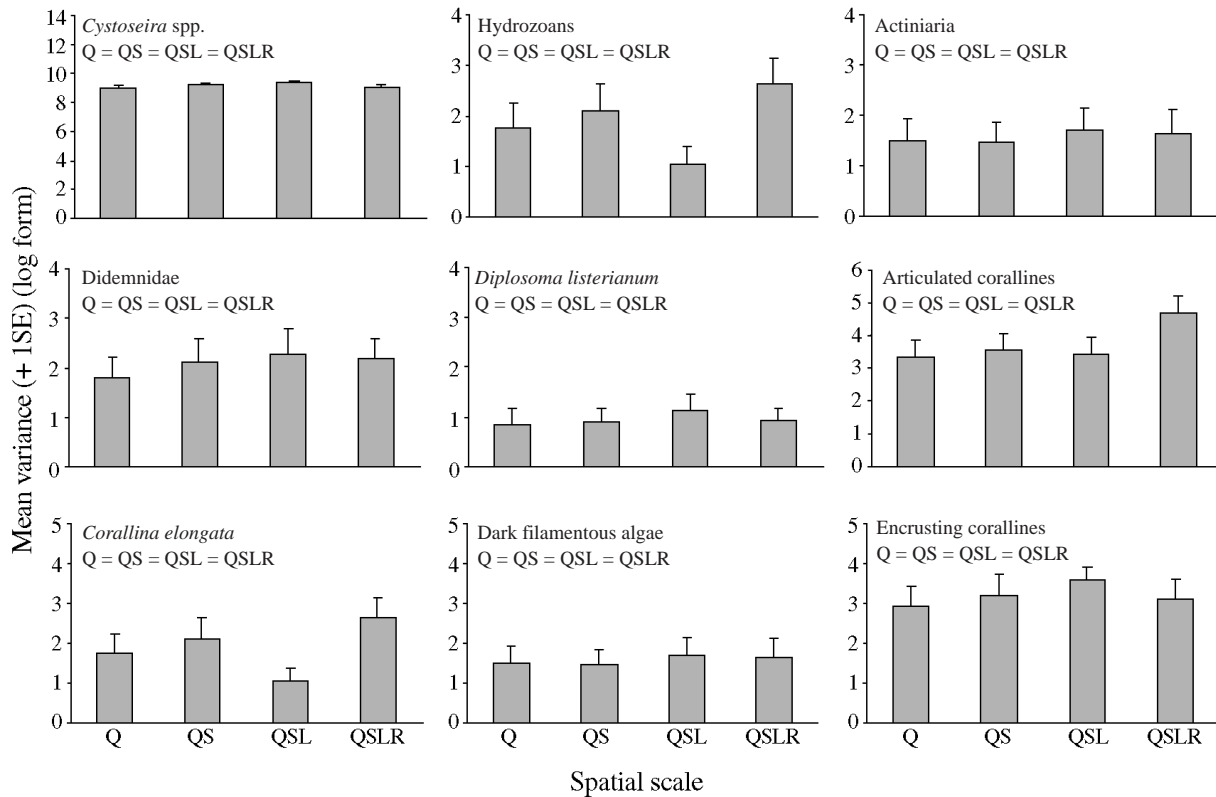
Fig. 5. Mean (+SE, n = 24) estimates of variance in abundance (log form) of algae and invertebrates at 4 spatial scales in low-shore habitat. Results of SNK tests comparing variances at different scales are included; abbreviations as in Fig. 3

several kilometers apart, whilst species with direct development were more variable among sites 100s of meters apart. The extent to which the life-history attributes of species and methodological issues affect our perception of the importance of scale is worthy of further scrutinity.

We posed 2 questions at the beginning of this study: (1) To what extent does small-scale variability contribute to large-scale patterns of variation? (2) Is there a pattern of variability that can be generalised across species and habitats? We now explore the extent to which the results of our field study clarify to these issues.

The null hypothesis that spatial patterns were invariant to scale was rejected in our study both for the midshore and the lowshore habitats, although patterns differed between heights on the shore and also depended on the taxa examined. In the midshore habitat, PERMANOVA revealed differences in the structure of assemblages from location to location and from site to site, but no difference at the regional scale. The same result was achieved by ANOVAs for most of the response variables analysed, where no term above the level of site was significant. This suggested that similar processes operated at midshore heights over broad

geographical scales. While local patterns were complex, the structure of the assemblage and the distribution of single taxa could be related across space from local to regional scales, suggesting that, at least in this habitat, the findings of small-scale studies may be scaled up to larger areas in agreement with the findings of other studies (Thrush et al. 1997a, Irving et al. 2004). Physical stress in the harsh midshore environment could possibly limit the large-scale variability observed in other habitats (Jackson 1977, Archambault & Bourget 1996).

The lowshore habitat was heterogeneous at all scales considered. This result indicated that patterns could not be generalised in space for this habitat (Jackson 1977, Crowe & Underwood 1999) and suggested caution in using the results of small-scale experiments to explain patterns over broad spatial extents (Foster 1990, Brown 1995, Connolly & Roughgarden 1998).

The general result from the analysis of variance components was in agreement with the results from the survey of the literature, where most variation in patterns of abundance was at the smallest spatial scale. This pattern was observed, with no exception, for all variables examined in each habitat. Of course, these findings are contingent on the specific time at which

the study was conducted. Temporal replication is needed before drawing any general conclusion, since spatial patterns do not necessarily remain constant over time (Underwood & Petraitis 1993).

Other authors have addressed the issue of whether local variability can scale up to generate large-scale patterns. Thrush et al. (1997a) and Wootton (2001) provided some evidence that patterns of complexity can be related across space from local to regional scales (1000s of kilometers). Furthermore, Fowler-Walker & Connell (2002) showed consistent biodiversity patterns over biogeographic scales despite enormous spatial variability at smaller spatial scales. Hughes et al. (2002), in order to derive large-scale biodiversity patterns in space or time from small-scale descriptive data, linked experimental data to a meta-analysis of a vast array of information on coral reef distribution, suggesting that this procedure might be of general relevance. Connolly & Roughgarden (1998) demonstrated that attempts to synthesise regional differences in the structure of assemblages could largely benefit from considering both the benthic adult and pelagic larval environments. Although important, we believe these examples are still preliminary and, along with the results of our analysis, they show that scaling-up effects are likely to be context-dependent. Consequently, we believe it is still premature to derive general conclusions on scaling-up effects in marine assemblages.

Our data did not reveal consistent patterns of spatial variation at intermediate scales (from 10s of meters to 10s of kilometers). This situation is also common in the literature, although in a few cases small-scale variability declines progressively (rather than abruptly) with increasing spatial scales of sampling (e.g. Underwood & Chapman 1996, Olabarria & Chapman 2001). Indeed, patterns of variation in published studies range from cases in which variability occurs at all scales (e.g. Menconi et al. 1999, Coleman 2002), to cases in which variation is concentrated mostly at a particular scale, as already discussed (e.g. Archambault & Bourget 1996, Hyder et al. 1998, Hughes et al. 1999, Kendall & Widdicombe 1999). These results confirm the absence of any single appropriate scale at which populations and assemblages should be investigated, forcing ecologists to adopt a multi-scale approach in analyses of spatial and temporal patterns (Levin 1992, Hewitt et al. 1998).

Documenting the spatial scales at which significant differences in abundances of organisms are found allows the formulation of hypotheses about the relevant processes, which may determine these patterns (Underwood & Chapman 1996). However, such documentation requires proper evaluation of the efficiency of different methods. In our case, the use of 2 proce-dures was justified by the need to measure variability with the same precision at different scales. Both methods revealed considerable more variability at the scale of replicate quadrats than at the other scales. A difference, however, existed between the methods in the outcome of univariate analyses of lowshore assemblages. Hierarchical ANOVAs revealed significant spatial variation at all scales in lowshore assemblages, whereas pairwise comparisons failed to detect differences above the scale of replicate quadrat. Both methods detected significant variation at small and large spatial scales for multivariate data. To some extent, these results justify the use of a nested analysis of variance to detect patterns at the top of the hierarchy when the immediate lower level is properly replicated. By sampling 7 locations in each region we guaranteed enough power to detect large-scale effects that were not so easily detected in the pairwise comparisons.

Identifying relevant scales of variability, along with the development of innovative statistical techniques (Underwood & Chapman 1998a, Legendre et al. 2002), is crucial for implementing monitoring programs and environmental impact studies (Thrush et al. 1994, Schoch & Dethier 1996, Bishop et al. 2002). Small-scale variability has several implications for understanding patterns and processes and in the analysis of environmental impacts. Patchiness may reduce the power of statistical tests, thus calling for careful optimization of experimental design of environmental sampling programs (Benedetti-Cecchi 2001b, Underwood & Chapman 2003). Changes in small-scale variability have been repeatedly proposed as a diagnostic feature of disturbed marine assemblages (Caswell & Cohen 1991, Warwick & Clarke 1993). However, since large variability characterises also non-impacted assemblages, adequate reference conditions should always be used when interpreting variability in disturbed environments.

In conclusion, there is still a need to investigate the spatial pattern of ecological variables in a wider range of habitats and on a larger number of species in marine coastal areas. To date, the only scale that we possibly define as 'critical' or 'characteristic' is that between replicate units, and this small-scale variability is possibly one of the few common patterns between terrestrial and marine habitats. Notwithstanding frequent literature reports, small-scale variability is not 'noise' determined by nonspecific 'stochastic' processes. Rather, patchiness underlies a complex suite of factors that possibly change from place to place and time to time (Coleman et al. 2004). Recognizing the pervasive nature of small-scale spatial variation will be important in understanding causal linkages between patterns and processes and in developing better experimental and sampling designs to unravel these relationships in

future studies. We suggest that this pattern is common to a wide range of natural systems where assemblages are influenced by complex sets of physical and biological processes such as those operating in the marine environment.

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