



Variation in rocky shore assemblages in the northwestern Mediterranean: contrasts between islands and the mainland

L. Benedetti-Cecchi^{a,*}, E. Maggi^a, I. Bertocci^a, S. Vaselli^a,
F. Micheli^b, G.C. Osio^{a,b}, F. Cinelli^a

^a*Dipartimento di Scienze dell'Uomo e dell'Ambiente, Via A. Volta 6, I-56126 Pisa, Italy*

^b*Hopkins Marine Station, Stanford University, Pacific Grove, CA, USA*

Received 1 July 2002; received in revised form 7 April 2003; accepted 29 April 2003

Abstract

Insular assemblages of species are often considered unique because they are exposed to unpredictable patterns of colonization/extinction that depend on distance from other sources of colonists and on size of islands. An alternative explanation is that islands provide fundamentally different habitats of those of the mainland, regardless of any possible effect of size and isolation. These alternatives were examined by comparing assemblages of rocky shores on islands of the Tuscan Archipelago with those of the mainland in the same geographical region. Sandy beaches created a pattern of discrete areas of rock along the mainland with spatial discontinuities and extents comparable to those of the insular environment. Possible effects of isolation and size were therefore controlled in this study, so that one would expect no difference between islands and the mainland if only size and isolation matter. In contrast, differences are expected if historical events or other processes have distinct influences on assemblages in these environments. These hypotheses were tested by comparing assemblages of midshore and lowshore habitats of two islands with those of two similarly distributed locations on the mainland over a period of 2 years, using a hierarchical sampling design. Multivariate and univariate analyses revealed various patterns in the data. There were differences between islands and the mainland in structure of assemblages, in mean abundance of common taxa and in the magnitude of spatial and temporal variance in abundance in both habitats. Collectively, these findings support the model that islands in the Tuscan Archipelago have distinct assemblages from the mainland, thereby contributing to the

* Corresponding author. Tel.: +39-50-500943; fax: +39-50-49694.

E-mail address: bencecc@discat.unipi.it (L. Benedetti-Cecchi).

regional diversity and complexity of assemblages of rocky shores over and above any possible effect of size or isolation.

© 2003 Elsevier B.V. All rights reserved.

Keywords: Rocky shores; Island versus mainland comparisons; Algae; Invertebrates; Spatial variance; Temporal variance; Structure of assemblages; Island biogeography

1. Introduction

The notion that natural populations fluctuate in abundance at various scales in space and time is well established in the ecological literature (Andrewartha and Birch, 1954; den Boer, 1968; Dayton and Tegner, 1984; Levin, 1992; Gaston and McArdle, 1993; Schneider, 1994). Although no obvious generalization has emerged, studies conducted in marine coastal habitats usually show considerable small-scale spatial patchiness (tens to hundreds of centimetres) for organisms living on hard substrata and soft bottoms (Morrisey et al., 1992; Commito et al., 1995; Archambault and Bourget, 1996; Underwood and Chapman, 1996; Williams et al., 2000; Benedetti-Cecchi, 2001; Fraschetti et al., 2001). At larger spatial scales, between tens and thousands of metres, spatial variation may or may not be relevant for these organisms. As a result, various patterns can be observed for different species within the same assemblage (e.g. Benedetti-Cecchi, 2001). At even larger scales (hundreds to thousands of kilometres), spatial variation can be expected to be large for many species, possibly due to the influence of a wide range of habitats and environmental conditions (but see Kennelly and Underwood, 1993; Chapman and Underwood, 1998).

Comparably fewer studies have examined variability at a hierarchy of temporal scales, or the extent to which space and time interact (e.g. Farnsworth and Ellison, 1996; Dayton et al., 1999). The difficulty of maintaining long-term research programmes often precludes the possibility of examining changes in assemblages beyond those occurring over a few years. Very few studies have enabled comparisons over larger temporal scales. Studies on barnacles, for example, have shown large changes in abundance at the scale of decades (Southward, 1991). Space \times time interactions, in contrast, are usually only quantified at the scale of month or year (e.g. Underwood, 1991; Menconi et al., 1999).

The analysis of pattern in distribution and abundance of organisms has direct relevance to the identification of underlying causal processes (Holling, 1992; Wiens et al., 1993; Wu and Loucks, 1995). Whereas some ecological processes are scale-specific, others may operate over a range of spatial or temporal scales. Biotic interactions and behaviour are generally implicated in the maintenance of small-scale spatial patchiness, whereas oceanographic conditions and climate largely dictate regional and long-term patterns (Smith and Buddemeier, 1992; Underwood and Chapman, 1996; Krönke et al., 1998; Thrush et al., 2000). Variation in dispersal and recruitment of organisms, in contrast, may occur over very different scales. Patchiness in the distribution of larvae in the water column, for example, may be responsible for small-scale spatial variation in density of adult barnacles (Grosberg, 1982). Limits to the dispersal capabilities of these populations

can, however, also affect their distribution over larger spatial scales (Caffey, 1985; Raimondi, 1990).

Islands have provided extremely valuable systems to test hypotheses about large-scale spatial patterns in assemblages, particularly when patterns on islands have been contrasted with those of the mainland. Differences between islands and the mainland have been described and identified mainly for terrestrial organisms (e.g. Sol, 2000), although several studies have been devoted to the ecology of marine coastal assemblages on islands (e.g. Dayton, 1975; Santelices and Ojeda, 1984; Konar, 2000; Benedetti-Cecchi et al., 2000, 2001). Insular assemblages are often considered unique because they are exposed to unpredictable patterns of colonization/extinction that depend on the distance from other sources of colonists and on size of islands (Mac Arthur and Wilson, 1967; see also den Boer, 1968).

An alternative, albeit not mutually exclusive explanation of the observed differences between islands and the mainland would be that islands provide environments that are fundamentally different from those of the mainland. Historical events, physical processes such as local oceanography and climate, natural and anthropogenic disturbance and biotic interactions, may, in principle, contribute to environmental heterogeneity in different ways on islands than on the mainland (reviewed by Brown and Lomolino, 2000).

Direct experimental tests of these two explanations can be difficult to conduct in marine systems, due to logistical constraints in manipulating dispersal of organisms, local climate and other physical features of the habitat. Before embarking in such an endeavour, it is therefore important to establish quantitative, objective observations about possible differences between islands and the mainland, particularly in those habitats where subsequent experimental manipulations would be more feasible, like rocky seashores.

In this study, we compare assemblages from midshore and lowshore habitats of rocky coasts of two islands in the Tuscany Archipelago, with those of two locations on the mainland. Rocky areas occur as discrete units also on the mainland in this geographical region and can reasonably be considered as 'islands' in terms of spatial extent and distance from other rocky shores. Fragmentation on the mainland is provided by sandy beaches that create a pattern of distances among rocky areas similar to the range of distances separating the various islands in the Archipelago. Thus, possible effects of isolation and size that might dictate differences between assemblages of islands with those of the mainland were controlled in this study. If islands provided fundamentally different environments of those of the mainland, then it should still be possible to observe differences in assemblages between the two contrasting conditions over and above any possible effect of size and isolation. If, in contrast, the peculiarity of islands is determined by traits such as isolation and size, then one would expect large differences among islands and among locations on the mainland, but no difference, on average, between these conditions. Under this scenario, one would also predict similar patterns of spatial and temporal variation between islands and the mainland at comparable scales. These hypotheses were tested with a multifactorial sampling design and with univariate and multivariate methods of analysis.

2. Materials and methods

2.1. Study locations and organisms

This study was undertaken between June 1999 and March 2001 on two islands of the Tuscany Archipelago (Capraia and Giannutri) and at two locations on the mainland (Calafuria and Argentario, Fig. 1). Capraia and Giannutri are part of the National Park of the Tuscany Archipelago, a network of Marine Protected Areas established in 1996 (Benedetti-Cecchi et al., 2003). Capraia is the northern of the two islands and has 27 km of

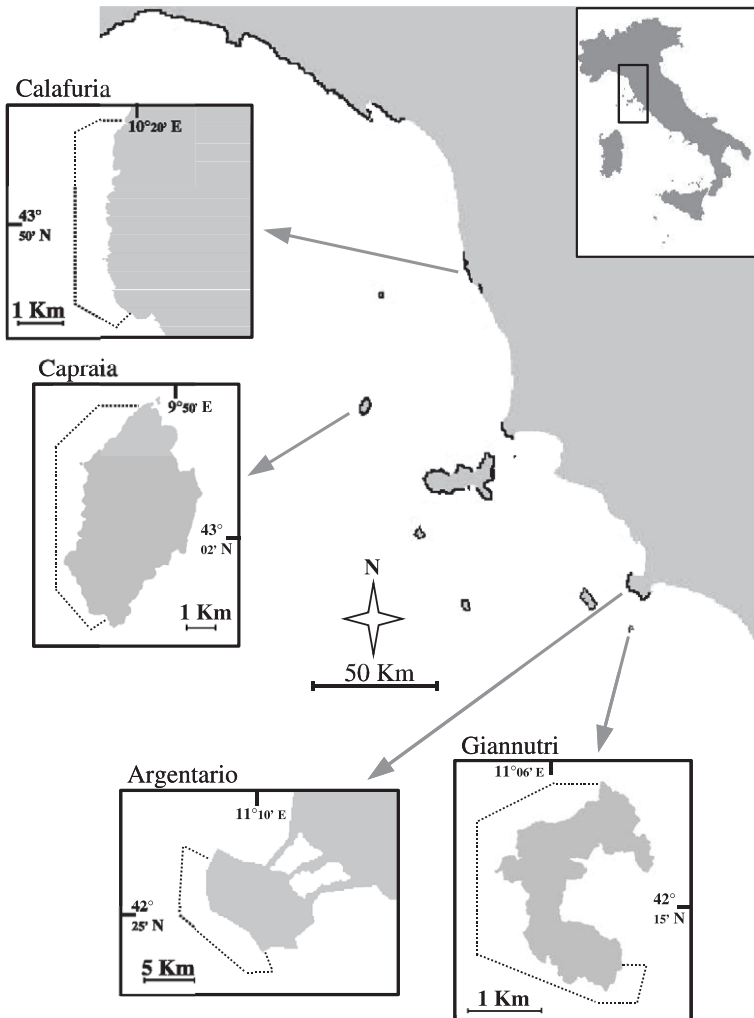


Fig. 1. Map of the study area. Black contours of the coastline indicate rocky sea shores. Dotted lines delimit the areas within which the sampling sites were randomly chosen.

volcanic shores. Giannutri is the southernmost island of the Archipelago and has 11 km of calcareous shores. Calafuria is a rocky area of about 5 km that extends to the north into the city of Livorno. It is connected in the south to another rocky area of similar size (Castiglioncello, not included in the study) by a series of cobble beaches and a small marina. The substratum is mostly sandstone and this location has been intensively investigated in the last 10 years (e.g. Benedetti-Cecchi, 2000). Argentario is a promontory facing the island of Giannutri made up of a large outcrop of various kinds of rock (schists, metamorphic and calcareous rocks) with nearly 30 km of rocky shores.

Capraia and Giannutri are about 150 km apart, a distance similar to that separating Calafuria from Argentario. Each of these locations (whether island or mainland) is at least 20 km away from other rocky areas. Sandy beaches create major discontinuities among rocky areas on the mainland (Fig. 1). The degree of isolation of Calafuria and Argentario is therefore comparable to that of the two islands. Furthermore, although there are differences in size between the two locations on the mainland and the two islands, there is no substantial difference in average spatial extent of rocky areas between the two environments.

All shores supported similar assemblages of algae and invertebrates. The most common organisms in the midshore habitat were filamentous algae such as *Polysiphonia sertularioides* (Grateloup) and *Chaetomorpha aerea* (Dillwyn) Kützing, encrusting corallines, the encrusting brown alga *Ralfsia verrucosa* (Areshoug) J. Agardh, the fleshy alga *Rissoella verruculosa* (Bertolini) J. Agardh and cyanobacteria (*Rivularia* spp.). Invertebrates included the barnacle *Chthamalus stellatus* (Poli), the limpets *Patella rustica* L. and *Patella aspera* (Röding) and the topshell *Osilinus turbinatus* (Von Born).

Lowshore assemblages included those dominated by canopy algae such as *Cystoseira amentacea* Bory var. *stricta* Montagne and sessile invertebrates (mainly sponges, hydrozoans, bryozoans and actinians), and those dominated by turf-forming algae. The latter were characterised by geniculate coralline algae such as *Corallina elongata* Ellis et Solander and *Haliptilon virgatum* (Zanardini) Garbary and Johansen, coarsely branched algae like *Laurencia* spp., *Chondria* spp. and *Gastroclonium clavatum* (Roth) Ardissonne and several species of filamentous algae. Grazers such as limpets and sea urchins were rare in the lowshore habitat at the study sites. Further descriptions of these assemblages can be found in related studies (Menconi et al., 1999; Benedetti-Cecchi, 2001; Benedetti-Cecchi et al., 2001).

2.2. Sampling design and collection of data

Two habitats were sampled: the midshore habitat, approximately between 0.2 and 0.4 m above mean-low-water-level (MLWL) and the lowshore habitat, approximately between –0.1 and 0.1 m with respect to the MLWL. The sampling design consisted of two replicate locations (hereafter the term location will also be used to refer to the two replicate islands, when appropriate) for each level of the Island vs. Mainland contrast. Each location was sampled four times over a period of nearly 2 years (June 1999–March 2001), but dates differed among locations because logistical constraints prevented simultaneous sampling at any given point in time. The 16 dates of sampling (4 dates \times 4 locations) were, however, interspersed in the study period, so that effects of location and time were

not confounded. Six replicate sites (stretches of coast of 20–30 m) were selected randomly at each location on each time and for each habitat. Sites were distributed along several kilometres of shores (Fig. 1) and eight random quadrats of 20 × 20 cm were sampled in each site. On islands, sampling sites were concentrated as much as possible on the western coasts to maintain consistency with the geographical orientation of sites on the mainland. A few sites, however, faced either northwest or southeast and this happened both on islands and on the mainland.

Data consisted of estimates of percent cover for sessile organisms (algae and invertebrates) and number of individuals per quadrat for mobile animals (limpets). Percent cover estimates were obtained visually, by dividing each quadrat into 25 sub-quadrats of 4 × 4 cm and assigning to each of them a score from 0 (absence of a particular taxon) to 4 (the sub-quadrat was totally covered by a particular taxon) and adding up the 25 estimates (Dethier et al., 1993).

2.3. Analysis of data

Locations were treated as a random factor in analyses. There was no specific a priori ecological reason for including any of these locations in the study; other islands and other locations on the mainland might have been used to compare the two environments, provided that degree of isolation and spatial extent did not confound the comparison. The only purpose of having two islands and two locations on the mainland was to provide a minimum degree of replication within each condition in order to construct an appropriate test for the main contrast of interest: island vs. mainland. Random selection of locations was, however, not possible due to a number of logistical constraints (for example, it would have been much more expensive to work on different islands). Furthermore, random selection of locations would not have guaranteed comparable patterns of isolation and spatial extent between islands and the mainland. The consequences of having not truly random locations must, however, be kept in mind when interpreting the results of this study at the regional scale.

Multivariate analyses were used to compare assemblages on islands with those of the mainland for each habitat separately. An 'average sample' was first obtained for each location and time of sampling by averaging data across sites and quadrats. A matrix of similarities between each pair of these samples was then calculated using the Bray–Curtis similarity coefficient on untransformed data (Bray and Curtis, 1957). Two-way nested ANOSIM (Clarke, 1993) was performed to test for differences between islands and mainland and among locations, using the four times of sampling as replicates. Because there are only three possible permutations for the Island vs. Mainland comparison, only the *R* statistic is reported for these tests with no associated probability. Non-metric multidimensional scaling (nMDS) was used to produce two-dimensional ordinations of the rank orders of similarities in each habitat (Field et al., 1982; Clarke, 1993; Anderson and Underwood, 1997).

Analysis of variance was used to test the hypothesis that the mean abundance of common taxa differed between islands and the mainland and to compare patterns of variation at different scales between the two environments. Factors in analyses were: Island vs. Mainland (fixed, two levels), Location (random, two levels, nested within the

Island vs. Mainland comparison), Time (random, four levels, nested within Location and Island vs. Mainland) and Site (random, six levels, nested within Time, Location and Island vs. Mainland). Analyses were done for each habitat separately. Cochran's C test was used to check the assumption of homogeneity of variances and, when necessary, data were log-transformed to remove heterogeneous variances. In cases where homogeneity was not achieved, analysis of raw data was still conducted as the procedure is robust to departures from this assumption when there are several independent estimates of residual variance (Underwood, 1997).

Analysis of variance was also used to estimate variance components at three spatial scales (among quadrats, among sites and among locations) and temporal variance in each habitat, separately for islands and the mainland. Estimates were obtained by equating observed and expected mean squares for the specific model of analysis (Winer et al., 1991; Underwood, 1997). Negative estimates were assumed to be sample underestimates of zero variances (Searle et al., 1992; Underwood, 1996), but actual values are presented in tables. Two-tailed F ratios on non-negative variances were used to test the null hypothesis of no difference between islands and the mainland in patterns of spatial and temporal variation of common taxa. Untransformed data were used in these analyses.

3. Results

3.1. Midshore habitat

The nested analysis of similarity (ANOSIM) revealed significant differences in structure of assemblages among locations ($R=0.99$, $P<0.003$), whereas the magnitude of the difference between islands and the mainland was lower ($R=0.5$). The nMDS plot

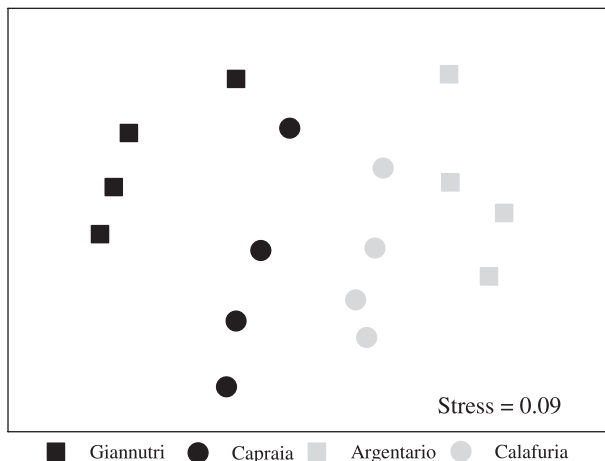


Fig. 2. nMDS plot comparing midshore assemblages of two locations on the mainland with those of two islands of the Tuscany Archipelago. Each symbol is the 'average sample' obtained by averaging across quadrats and sites at each sampling occasion.

Table 1
Analysis of variance on abundance of algae and invertebrates in the midshore habitat

Algae											
Source of variation	df	Encrusting corallines		Filamentous algae		<i>Lithophyllum lichenoides</i>		<i>Rissoella verruculosa</i>		<i>Rivularia</i> spp.	
		MS	F	MS	F	MS	F	MS	F	MS	F
Island vs. Mainland=I	1	116.0	1.6	43.663	4.7	312.6	2.2	217.7	6.0	2037.8	0.8
Location(I)=L(I) ^a	2	72.4	17.4***	9.322	0.8	142.9	47.0***	36.2	3.3	2731.6	2.5
Time(L(I)) ^b	12	4.1	1.5	12.152	4.6***	3.0	1.5	10.8	2.5**	1085.1	2.7***
Site(Time(L(I))) ^c	80	2.8	2.5***	2.660	2.9***	2.1	4.6***	4.3	5.5***	404.9	2.2***
Residual ^d	672	1.1		0.922				186.4			0.4
Cochran's C test		C=0.03	ns	C=0.04	ns	C=0.05	ns	C=0.05	ns	C=0.04	ns
Transformation		ln(x+1)		ln(x+1)		ln(x+1)		ln(x+1)		none	
Invertebrates											
Source of variation	df	<i>Chthamalus</i> spp.		<i>Patella aspera/caerulea</i>		<i>Patella rustica</i>					
		MS	F	MS	F	MS	F				
Island vs. Mainland=I	1	64,039	11.6	0.13	0.0	8.179	0.2				
Location(I)=L(I) ^a	2	5523	6.1*	64.19	4.8*	43.765	47.3***				
Time(L(I)) ^b	12	905	0.6	13.28	2.4*	0.925	1.0				
Site(Time(L(I))) ^c	80	1528	6.6***	5.57	2.1***	0.900	2.4***				
Residual ^d	672	231		2.60		0.368					
Cochran's C test		C=0.05	ns	C=0.06	ns	C=0.03	ns				
Transformation		none		none		ln(x+1)					

ns = not significant.

^a Denominator for I.

^b Denominator for L(I).

^c Denominator for Time(L(I)).

^d Denominator for Site(Time(L(I))).

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

clearly distinguished among all locations, but also separated assemblages of islands from those of the mainland (Fig. 2). There was also large temporal variation within this habitat, as indicated by the spread of the replicate ‘average samples’ in the nMDS plot.

Univariate analyses indicated no significant effect of the contrast of Island vs. Mainland for any of the taxa investigated (Table 1). This was in part a consequence of the large and significant variation among locations and likely reflects low statistical power for the main

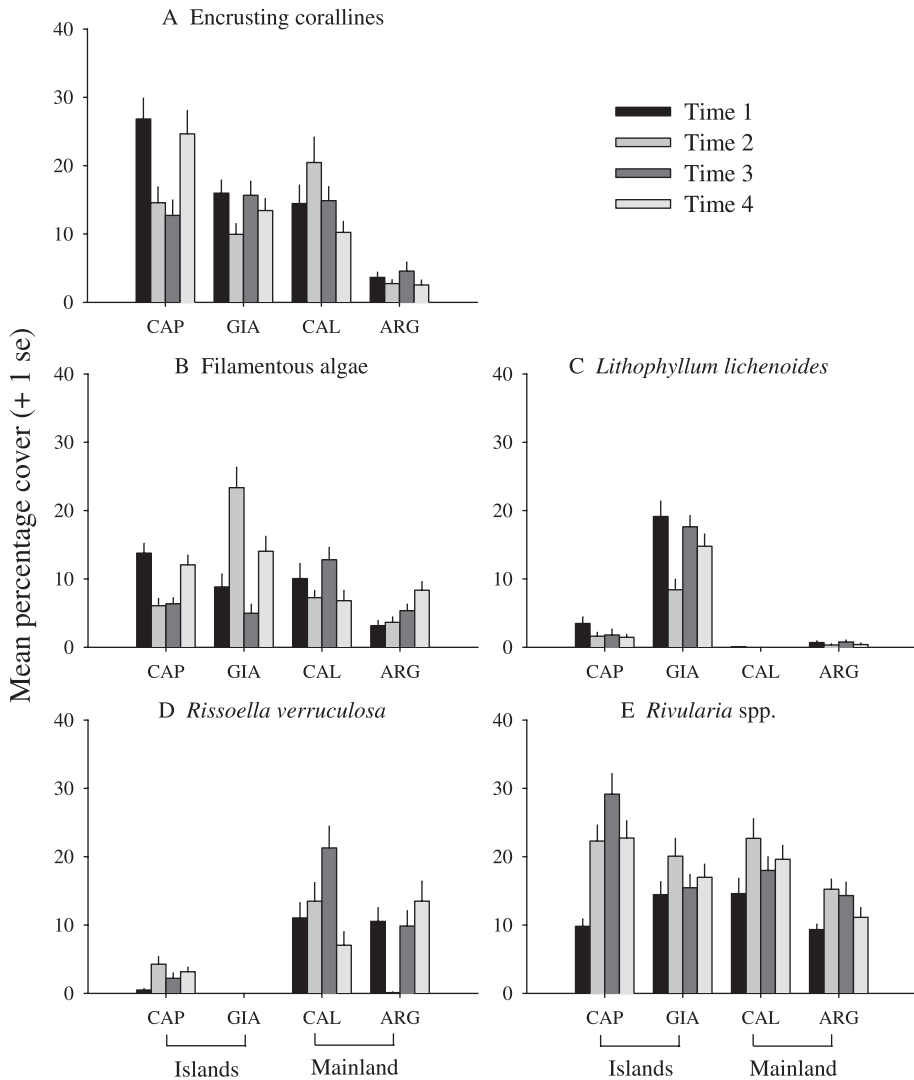


Fig. 3. Mean percentage cover (± 1 S.E., $n=48$) of algae in the midshore habitat. Data are shown at each of four sampling times in each of two islands and two locations of the mainland. Values have been pooled across sites and quadrats in each location. CAP: Capraia; GIA: Giannutri; CAL: Calafuria; ARG: Argentario.

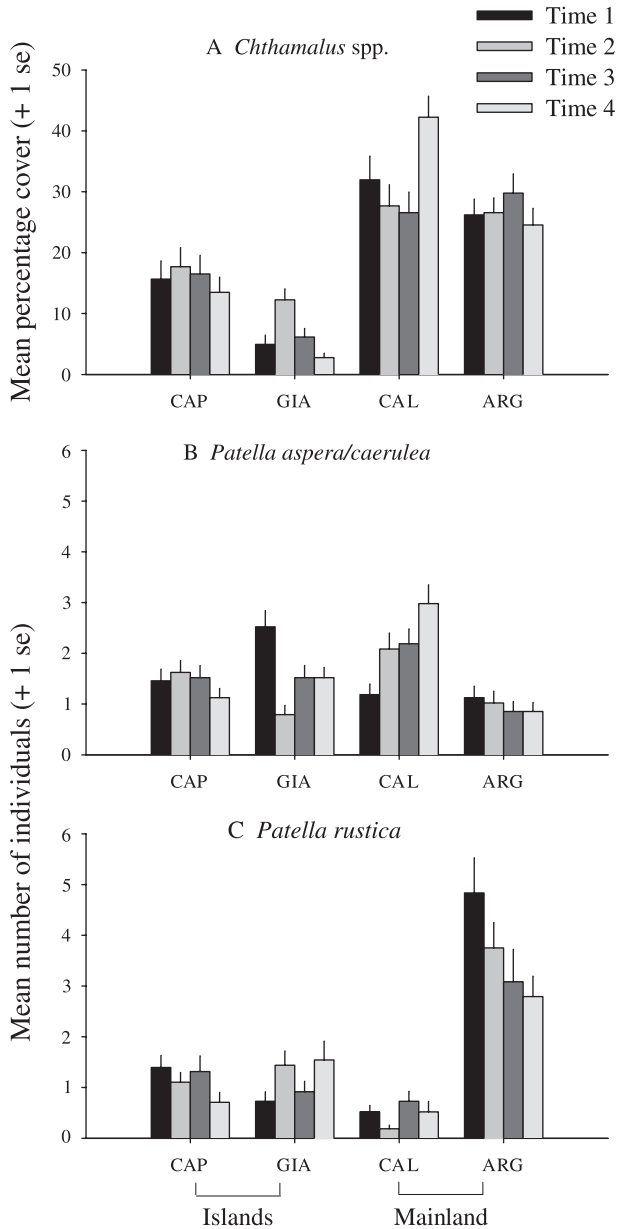


Fig. 4. Mean percentage cover (+1 S.E., $n = 48$) of invertebrates in the midshore habitat. Data are shown at each of four times of sampling in each of two islands and two locations of the mainland. Values have been pooled across sites and quadrats in each location. Abbreviations as in Fig. 3.

Table 2

Estimates of variance components and two-tailed *F* ratios comparing patterns in spatial and temporal variance between islands and the mainland in midshore habitat

	Source of variation											
	Location (<i>df</i> 1,1)			Time(Location) (<i>df</i> 6,6)			Site(Time(Location)) (<i>df</i> 40,40)			Quadrat(Site(Time(Location))) (<i>df</i> 336,336)		
	M	I	Test	M	I	Test	M	I	Test	M	I	Test
<i>Algae</i>												
Encrusting corallines	65.321	10.431	ns	- 1.322	16.056	-	44.795	48.993	ns	148.535	224.921	I>M***
Filamentous algae	6.807	- 4.596	-	3.425	28.157	I>M*	8.850	54.389	I>M***	83.159	103.289	I>M*
<i>Lithophyllum lichenoides</i>	0.138	80.297	ns	- 0.062	5.112	-	0.386	31.157	I>M***	0.993	66.224	I>M***
<i>Rissoella verruculosa</i>	2.398	2.898	ns	19.299	0.692	M>I***	68.136	2.007	M>I***	205.656	12.032	M>I***
<i>Rivularia</i> spp.	17.040	0.112	ns	2.295	26.047	I>M**	22.715	31.894	ns	161.460	211.372	I>M*
<i>Invertebrates</i>												
<i>Chthamalus</i> spp.	7.255	40.855	ns	- 4.005	- 21.958	-	146.261	177.809	ns	359.804	103.390	M>I***
<i>Patella aspera/caerulea</i>	0.587	- 0.057	-	0.125	0.197	ns	0.574	0.167	M>I***	2.760	2.444	ns
<i>Patella rustica</i>	4.774	- 0.031	-	0.055	0.021	ns	1.373	0.261	M>I***	7.283	2.925	M>I***

M = mainland; I = island; ns = not significant. There is no test for negative variance components.

* $P < 0.05$.** $P < 0.01$.*** $P < 0.001$.

contrast. Although not significant, F ratios of the contrast of Island vs. Mainland were large for *R. verruculosa* and barnacles and these organisms were apparently more abundant on the mainland than on islands (Figs. 3D and 4A). Temporal variation was large and significant for filamentous algae, *R. verruculosa* and *Rivularia* spp. among algae (Table 1, Fig. 3B,D,E), and for *P. asper/caerulea* among invertebrates (Table 1, Fig. 4B). Spatial variation among sites was large and significant in all the analyses (Table 1).

There were similar patterns of spatial variance between islands and the locations on the mainland for the taxa examined, with the possible exception of *Lithophyllum lichenoides* which was more variable between islands (Table 2, Fig. 3). The pattern observed for *L. lichenoides* was, however, not significant and was paralleled by low values of mean abundance of this alga on the mainland (Fig. 3). There was larger temporal and spatial variation at the scales of site and quadrat on islands than on the mainland for *R. verruculosa*, and this was matched by the low abundance of this alga on islands (Fig. 3, Table 2). All other significant patterns for algae indicated more variation, whether spatial or temporal, on islands than on the mainland (Table 2). This was particularly evident at the scale of quadrat and for taxa that had similar patterns of abundance between islands and the mainland, such as filamentous and encrusting coralline algae and *Rivularia* spp. (Table 2, Fig. 3).

Invertebrates fluctuated more on the mainland, in contrast to observations for algae. Significant differences were detected at the scale of site for limpets and at the scale of quadrat for *Chthamalus* spp. and *P. rustica*, but not for *P. asper/caerulea* (Table 2). Patterns of variance in abundance of barnacles and *P. rustica* were paralleled by differences in mean values between the two environments, whereas this was not the case for *P. aspera* that occurred in similar numbers on islands and on the mainland (Fig. 4).

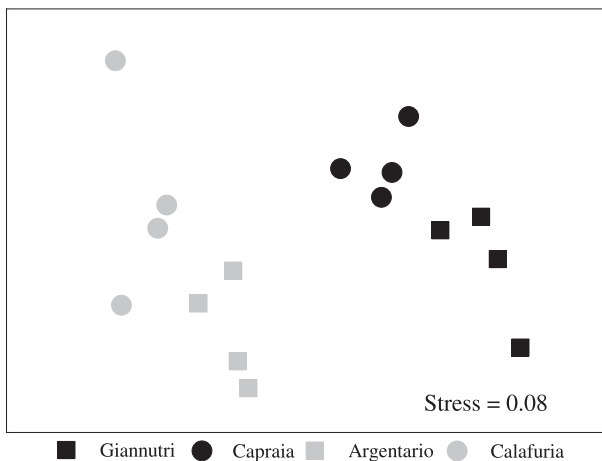


Fig. 5. nMDS plot comparing lowshore assemblages of two locations of the mainland with those of two islands of the Tuscany Archipelago. Each symbol is the 'average sample' obtained by averaging across quadrats and sites in each sampling occasion.

Table 3
Analysis of variance on abundance of algae and invertebrates in the lowshore habitat

Algae																
Source of variation	df	Articulated corallines		Coarsely branched algae		<i>Cystoseira amentacea</i>		<i>Cystosiera compressa</i>		Encrusting corallines		Filamentous algae		<i>Valonia utricularis</i>		
		MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	
Island vs. Mainland=I	1	41.470	0.8	223.167	36.2*	294,063	12.1	6.709	0.5	265.180	27.5*	120.687	7.1 ^{a,*}	14,822	1.6	
Location(I)=L(I)	2	53.445	2.8	6.162	0.5	24,399	8.1**	13.317	3.4	9.635	2.1	13.729	0.8	9319	12.2**	
Time(L(I))	12	19.050	3.6***	12.078	3.6***	3009	0.9	3.948	0.9	4.649	2.0*	17.154	5.0***	765	5.9***	
Site(Time(L(I)))	80	5.241	4.9***	3.356	3.3***	3545	7.1***	4.663	4.3***	2.293	2.4***	3.517	3.0***	132	2.2***	
Residual	672	1.073		1.005		497		1.086		0.961		1.047	3.4***	60		
Cochran's C test		C=0.03	ns	C=0.04	ns	C=0.05	ns	C=0.04	ns	C=0.04	ns	C=0.02	ns	C=0.09	P<0.01	
Transformation		ln(x+1)		ln(x+1)		none		ln(x+1)		ln(x+1)		ln(x+1)		none		
Invertebrates																
Source of variation	df	Bryozoans		<i>Mytilus galloprovincialis</i>		<i>Patella aspera/caerulea</i>		Sponges		<i>Vermetus</i> sp.						
		MS	F	MS	F	MS	F	MS	F	MS	F					
Island vs. Mainland=I	1	313.91	25.6*	5573.91	3.4	112.55	2.1	858.52	1.8	36.13	7.2					
Location(I)=L(I)	2	12.27	0.1	1662.66	5.2*	54.19	13.1**	489.61	1.5	5.05	2.5					
Time(L(I))	12	90.46	6.4***	321.31	2.3**	4.13	1.1	329.41	5.4***	2.02	2.3*					
Site(Time(L(I)))	80	14.09	1.7***	116.40	2.3***	3.63	2.5***	61.46	2.8***	0.89	2.0***					
Residual	672	8.25		1.45		22.21		0.45								
Cochran's C test		C=0.24	P<0.01	C=0.23	P<0.01	C=0.25	P<0.01	C=0.27	P<0.01	C=0.03	ns					
Transformation		none		none		none	none	ln(x+1)								

ns = not significant. F ratios as in Table 1.

MS_{pooled} = 16.973 with 14 df.

^a Tested against the pooled term L(I) + Time(L(I)).

* P < 0.05.

** P < 0.01.

*** P < 0.001.

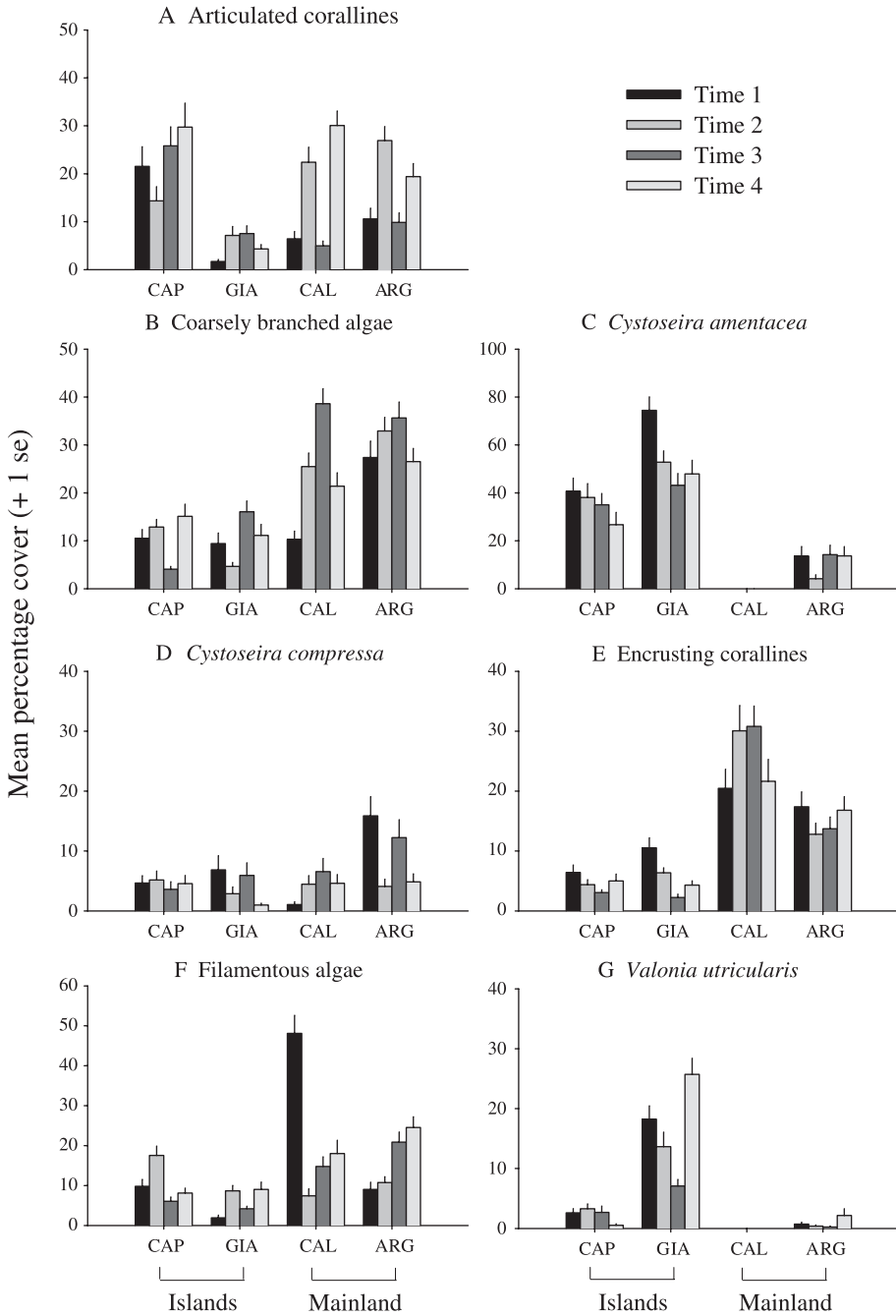


Fig. 6. Mean percentage cover (+ 1 S.E., $n=48$) of algae in the lowshore habitat. Data are shown at each of four times of sampling in each of two islands and two locations of the mainland. Values have been pooled across sites and quadrats in each location. Abbreviations as in Fig. 3.

3.2. Lowshore habitat

There were large differences in structure of assemblages between islands and the mainland ($R=0.95$) as well as differences between locations ($R=0.69$, $P<0.003$, Fig. 5).

Distinct groups of algae characterised the lowshore habitat on the mainland compared to those on islands. Coarsely branched, encrusting coralline and filamentous algae were

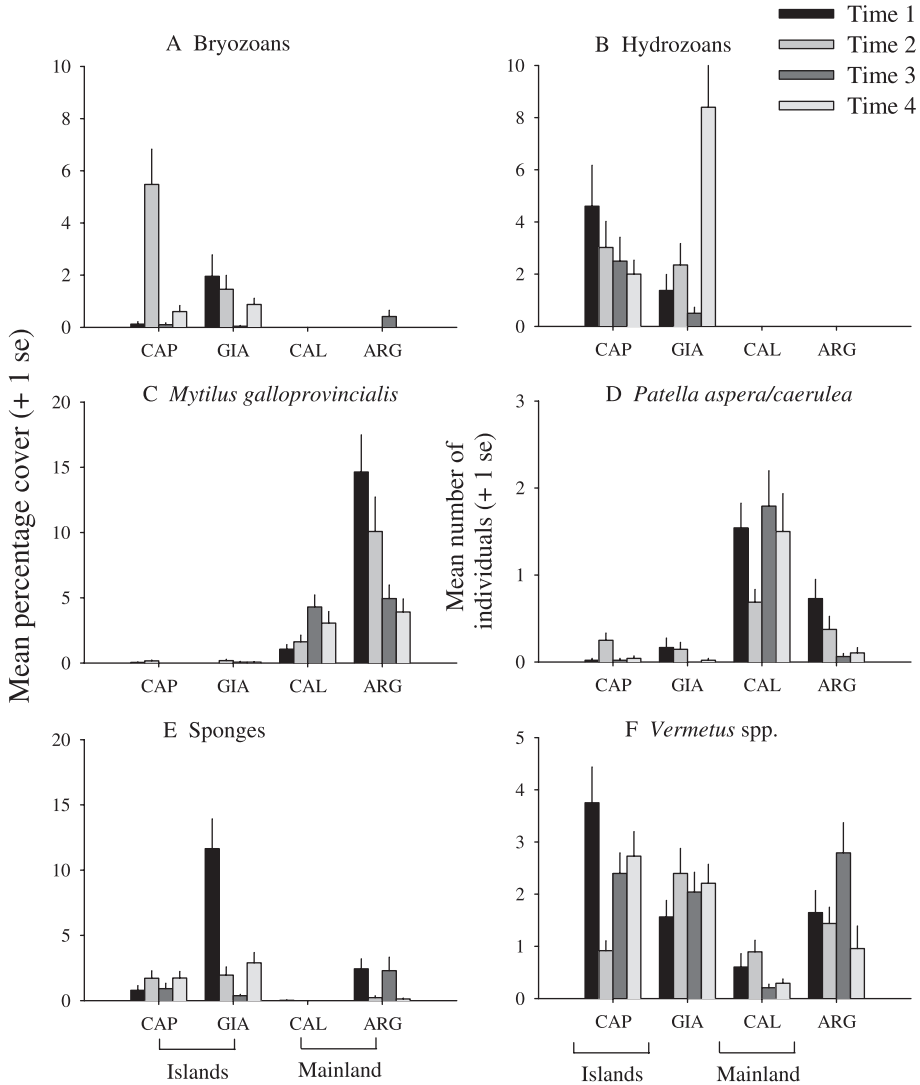


Fig. 7. Mean percentage cover (+1 S.E., $n=48$) of invertebrates in the lowshore habitat. Data are shown at each of four times of sampling in each of two islands and two locations of the mainland. Values have been pooled across sites and quadrats in each location. Abbreviations as in Fig. 3.

Table 4

Estimates of variance components and two-tailed *F* ratios comparing patterns in spatial and temporal variance between islands and the mainland in lowshore habitat

	Source of variation											
	Location (<i>df</i> 1,1)			Time(Location) (<i>df</i> 6,6)			Site(Time(Location)) (<i>df</i> 40,40)			Quadrat(Site(Time(Location))) (<i>df</i> 336,336)		
	M	I	Test	M	I	Test	M	I	Test	M	I	Test
<i>Algae</i>												
Articulated corallines	−26.765	149.878	−	90.8074	−8.336	−	76.775	165.172	I>M*	217.044	300.176	I>M**
Coarsely branched algae	2.773	−5.543	−	56.039	14.262	ns	90.711	30.618	M>I***	325.309	144.819	M>I***
<i>Cystoseira amentacea</i>	62.126	160.688	ns	−22.059	−0.248	−	184.719	577.123	I>M***	142.801	852.067	I>M***
<i>Cystoseira compressa</i>	8.214	−0.918	−	7.520	−1.506	−	50.712	20.704	M>I***	147.113	93.265	M>I***
<i>Encrusting corallines</i>	51.501	−1.157	−	−2.514	5.233	−	73.244	6.502	M>I***	367.426	43.726	M>I***
<i>Filamentous algae</i>	−30.540	5.089	−	165.801	13.728	M>I**	105.920	17.895	M>I***	266.462	89.050	M>I***
<i>Valonia utricularis</i>	0.285	88.817	ns	−0.250	26.628	−	3.110	14.858	I>M***	5.975	115.124	I>M***
<i>Invertebrates</i>												
Bryozoans	0.000	−0.815	−	0.013	3.170	I>M***	0.014	1.444	I>M***	0.327	16.181	I>M***
<i>Mytilus galloprovincialis</i>	13.974	−0.001	−	8.536	0.002	M>I***	16.4999	0.009	M>I***	100.623	0.119	M>I***
<i>Patella aspera/caerulea</i>	0.524	−0.003	−	0.015	0.006	ns	0.542	0.003	M>I***	2.747	0.159	M>I***
Sponges	0.601	1.068	ns	0.317	10.848	I>M***	1.839	7.975	I>M***	8.494	35.919	I>M***
<i>Vermetus</i> sp.	0.642	−0.109	−	0.191	0.488	ns	0.307	0.514	ns	5.246	8.522	I>M***

M = mainland; I = island; ns = not significant. There is no test for negative variance components.

* $P < 0.05$.** $P < 0.01$.*** $P < 0.001$.

significantly more abundant on the mainland, whereas the canopy alga *Cystoseira amentacea* was more abundant on islands, although this effect was not significant ($0.05 < P < 0.1$, Table 3, Fig. 6). Large and significant variability among locations was observed for *C. amentacea* and *Valonia utricularis*, whereas significant differences among sites were detected for all algae (Table 3). Temporal changes in abundance were negligible for both species of *Cystoseira*, whereas large and significant changes occurred for the other algae (Table 3, Fig. 6).

Among invertebrates, mussels and limpets were more common on the mainland, whereas bryozoans and hydrozoans were more abundant on islands (Fig. 7). A significant contrast of Island vs. Mainland was observed for bryozoans (Table 3, Fig. 7A); hydrozoans were not analysed because these organisms were not recorded in samples collected on the mainland (Fig. 7B). Spatial variation was large and significant at the scale of location for mussels and limpets, whereas variation at the scale of site was significant for all invertebrates (Table 3). Similarly, there were significant temporal changes in abundance for all sessile invertebrates, but not for limpets (Table 3).

Spatial variation was larger on islands than on the mainland for articulated coralline algae, *C. amentacea* and *V. utricularis*, at the scales of site and quadrat (Table 4). Low spatial variation was matched by low values of mean cover for canopy algae and *V. utricularis* on the mainland. This was not, however, the case for the abundance of articulated corallines which were similar in the two environments (Fig. 6A). Coarsely branched algae, *C. compressa*, encrusting corallines and filamentous algae, in contrast, were more variable on the mainland at the scales of site and quadrat. Temporal variation was larger on the mainland for filamentous algae. Again, low estimates of spatial variation were paralleled by low values of mean cover for coarsely branched, encrusting coralline and filamentous algae, but not for *C. compressa*.

There was significantly larger temporal variation for bryozoans and sponges on islands than on the mainland, whereas the opposite pattern occurred for mussels (Table 4). Similarly, there was more spatial variation on islands for bryozoans and sponges at the scales of site and quadrat and for *Vermetus* sp. at the scale of quadrat. Mussels and limpets were more variable on the mainland at the scales of site and quadrat (Table 4). Most of these patterns were paralleled by differences in mean abundance of organisms between islands and the mainland (Fig. 7).

4. Discussion

The study indicated differences between the islands and the mainland in structure of assemblages and in spatial and temporal patterns in abundance of several taxa. Lowshore assemblages discriminated more than midshore assemblages between islands and the mainland. Canopy algae and associated sessile invertebrates characterised the lowshore habitat of islands, whereas coarsely branched algae, encrusting corallines, filamentous algae, mussels and limpets characterised the locations of the mainland. Assemblages were relatively simple in the midshore habitat, but some organisms still discriminated between islands and the mainland. Common organisms such as barnacles and the red alga *R. verruculosa* were consistently more abundant on the mainland, whereas the encrusting

alga *L. lichenoides* was more abundant on islands. Differences between locations were large and significant in both habitats, but midshore assemblages were more variable at this scale. In general, there was more spatial and temporal variance in abundance on islands than on the mainland in the midshore habitat. Such a clear pattern was not, however, observed lower on the shore, where differences were more taxon-specific.

Collectively, the findings of this study support the model that some processes relevant to assemblages of rocky shores operate differently between islands and the mainland. Isolation of islands does not explain the observed differences among assemblages. The degree of isolation was, in fact, comparable among rocky shore assemblages located on islands and on the mainland because sandy beaches fragmented and separated stretches of mainland rocky shores over similar spatial scales to the distances separating islands in the Archipelago.

Several ecological processes are likely to operate differently between islands and the mainland. Islands are, by definition, bodies of land surrounded by water. This may create differences with the mainland in local oceanography and climate which, in turn, affect patterns of dispersal, growth and survival of organisms (e.g. Alexander and Roughgarden, 1996). Islands may also provide a wider range of environmental conditions than that offered by the mainland at comparable scales. Exposure to waves can vary to a greater extent along the sides of an island than along the shores of the mainland. Finally, anthropogenic disturbance is generally reduced on islands, due to the remoteness and lack of extensive coastal development on these small Mediterranean islands.

Variation in the intensity of anthropogenic disturbance provides a plausible explanation for the observed differences in the structure of lowshore assemblages between islands and the mainland. All small islands in the Tuscany Archipelago are relatively pristine locations compared to rocky areas of the mainland, with little to no human pressure in midshore and lowshore habitats. Benedetti-Cecchi et al. (2001) found that canopy algae were virtually absent from urban areas in the region and that lowshore assemblages were dominated by turf-forming algae in the absence of *Cystoseira* canopies. Greater abundance of *C. amentacea* on islands than on the mainland may be a consequence of low human impacts at these locations. Other studies have indicated that algae in the genus *Cystoseira* are highly sensitive to anthropogenic disturbance and tend to disappear from areas exposed to sewage discharge (Hoffman et al., 1988; Rodríguez-Prieto and Polo, 1996; Díez et al., 1999).

A decline in cover of canopy algae has been documented at several locations around the world over the last 30 years (Littler and Murray, 1975; Thom, 1980; Seapy and Littler, 1982; Hoffman et al., 1988; Vogt and Schramm, 1991). Canopy algae are important components of assemblages of rocky shores because they provide habitat to several species of animals and plants whilst preventing the establishment of other sessile organisms (Dayton, 1985; Schiel and Foster, 1986; Johnson and Mann, 1988; Chapman, 1990). Disappearance of these structurally important species is often associated with drastic changes in the structure of assemblages, as testified by numerous experimental manipulations of canopy algae (e.g. Dayton et al., 1984, 1992; Johnson and Mann, 1988).

Experimental studies in the northwest Mediterranean have shown both local and regional effects of *C. amentacea*. This alga was locally important in maintaining spatially distinct assemblages in the lowshore habitat (Bulleri et al., 2002). At larger spatial scales,

experimental clearings indicated that canopy algae contribute to the maintenance of differences between urban and undeveloped areas (Benedetti-Cecchi et al., 2001). Assemblages of turf-forming algae, similar to those occurring in urban areas, occurred in relatively pristine locations after *C. amentacea* removal. Dominance of canopy algae at Giannutri and Capraia can explain the low cover of turf-forming algae (mainly coarsely branched and filamentous algae) at these locations and, therefore, lowshore assemblages structure between islands and the mainland.

Although patterns in rocky shore assemblages are consistent with the hypothesis that lower anthropogenic disturbance on islands may allow persistence of canopy algae and associated invertebrates, lack of historical data on these assemblages and of direct quantification of the intensity and distribution of disturbances on the islands and mainland make it impossible to conclusively link these observed patterns to human impacts.

Other factors, in addition to anthropogenic disturbance, were likely to differ between islands and mainland shores and may underlie patterns in assemblages. Currents, oceanographic patterns and the geomorphology of the coastline, are commonly invoked as causes of large-scale variation in abundance of organisms that disperse larvae in the water column (Gaines et al., 1985; Pineda, 1994; Bertness et al., 1996; Caley et al., 1996; Connolly et al., 2001). These processes might explain the larger abundance of barnacles on the mainland. Large variance in patterns of abundance at the regional scale is a distinctive feature of barnacles in the study area (Benedetti-Cecchi, 2001). It is possible that oceanographic events limit dispersal of larvae offshore, reducing recruitment of barnacles to island rocky shore. There are, of course, other possible explanations for the difference between islands and the mainland in abundance of barnacles, such as type and texture of the substratum (e.g. Raimondi, 1988) or, more likely, a combination of oceanographic processes and local features of the environment (Hutchinson and Williams, 2001).

Differences between islands and the mainland were also revealed by the comparison of spatial and temporal variances. These patterns matched those of mean abundance for some taxa, with larger variances corresponding to larger means. In other instances, however, there was no apparent relationship between the mean and the variance. Most algae that fell into this category exhibited larger temporal variability and larger spatial heterogeneity at the scales of quadrat and site on islands than on the mainland. In contrast, there was larger among-site variation on the mainland for midshore populations of the limpets *P. aspera/caerulea*, but no difference at the scale of quadrat. Once again, one can only speculate on the underlying causes of variation, which are likely to involve complex interactions among several physical and biological processes (e.g. Underwood, 1985). The spatial and temporal scales over which these processes operate are, however, those usually covered by ecological experiments. It will be possible, therefore, to devise critical field tests to explain the differences between islands and the mainland in patterns of variation of common taxa at these scales.

There were no significant differences between islands and the mainland in patterns of variation between locations. Two-tailed tests had very low power for this comparison, involving only one degree of freedom both for the numerator and the denominator of the *F* ratio. Inspection of graphs and estimates of variances, however, suggested some differences between environments. Encrusting coralline algae and *P. rustica* were, for example, more variable between locations on the mainland than between islands. Articulated

coralline algae, in contrast, were more variable between islands. Other differences in the magnitude of variance among locations were trivial, as they involved absence or low cover of organisms in one or the other environment (e.g. *C. amentacea* and *V. utricularis*).

Differences in assemblages between the insular environment and the mainland are expected either in relation to isolation and size of islands or, as an alternative but not mutually exclusive explanation, because of intrinsic differences in the relevant processes operating in the two environments. The scrutiny of these models is important in assessing the extent to which islands provide unique environments with no counterpart on the mainland, thereby contributing to the regional complexity of marine coastal areas. Our study system provided a unique opportunity to proceed with such a test, due to the occurrence of discrete areas of rock along the mainland with spatial discontinuities and extents comparable to those of islands. The results show that islands in the Tuscan Archipelago contribute to the regional diversity and complexity of assemblages of rocky seashores over and above any possible effect of size or isolation. These findings establish the observational basis for future experimental investigations to identify the processes that most contribute to differentiate the insular environment from that of the mainland. Finally, the results have also important implications for conservation of marine coastal assemblages and would indicate that inclusion of representative assemblages within systems of marine-protected areas requires targeting rocky shores both on the mainland and on islands.

Acknowledgements

We thank Gray Williams and his students for commenting on the manuscript. This research was supported by a grant from the 'Ente Parco dell'Arcipelago Toscano', the National Geographic Society Committee for Research and Exploration and a grant from the University of Pisa. [AU]

References

- Alexander, S.E., Roughgarden, J., 1996. Larval transport and population dynamics of intertidal barnacles: a coupled benthic/oceanic model. *Ecol. Monogr.* 66, 259–275.
- Anderson, M.J., Underwood, A.J., 1997. Effects of gastropod grazers on recruitment and succession of an estuarine assemblage: a multivariate and univariate approach. *Oecologia* 109, 442–453.
- Andrewartha, H.G., Birch, L.C., 1954. *The Distribution and Abundance of Animals*. Univ. Chicago Press, Chicago.
- Archambault, P., Bourget, E., 1996. Scales of coastal heterogeneity and benthic intertidal species richness, diversity and abundance. *Mar. Ecol., Prog. Ser.* 136, 111–121.
- Benedetti-Cecchi, L., 2000. Predicting direct and indirect effects during succession in a midlittoral rocky shore assemblage. *Ecol. Monogr.* 70, 45–72.
- Benedetti-Cecchi, L., 2001. Variability in abundance of algae and invertebrates at different spatial scales on rocky sea shores. *Mar. Ecol. Prog. Ser.* 215, 79–92.
- 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 north-west Mediterranean. *Oecologia* 123, 406–417.
- Benedetti-Cecchi, L., Pannacciulli, F., Bulleri, F., Moschella, P.S., Airoldi, L., Relini, G., Cinelli, F., 2001.

- Predicting the consequences of anthropogenic disturbance: large-scale effects of loss of canopy algae on rocky shores. *Mar. Ecol. Prog. Ser.* 214, 137–150.
- Benedetti-Cecchi, L., Bertocci, I., Micheli, F., Maggi, E., Fosella, T., Vaselli, S., 2003. Implications of spatial heterogeneity for management of marine protected areas (MPAs): examples from assemblages of rocky coasts in the northwest Mediterranean. *Mar. Environ. Res.* 55, 429–458.
- Bertness, M.D., Gaines, S.D., Wahle, R.A., 1996. Wind-driven settlement patterns in the acorn barnacle *Semibalanus balanoides*. *Mar. Ecol. Prog. Ser.* 137, 103–110.
- Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of Southern Wisconsin. *Ecol. Monogr.* 27, 325–349.
- Brown, J.H., Lomolino, M.V., 2000. Concluding remarks: historical perspective and the future of island biogeography theory. *Glob. Ecol. Biogeogr.* 9, 87–92.
- Bulleri, F., Benedetti-Cecchi, L., Acunto, S., Cinelli, F., Hawkins, S.J., 2002. The influence of canopy algae on vertical patterns of distribution of low-shore assemblages on rocky coasts in the northwest Mediterranean. *J. Exp. Mar. Biol. Ecol.* 267, 89–106.
- Caffey, H.M., 1985. Spatial end temporal variation in the settlement and recruitment of intertidal barnacles. *Ecol. Monogr.* 55, 313–335.
- Caley, M.J., Carr, M.H., Hixon, M.A., Hughes, T.P., Jones, G.P., Menge, B.A., 1996. Recruitment and the local dynamics of open marine populations. *Ann. Rev. Ecol. Syst.* 27, 477–500.
- Chapman, A.R.O., 1990. Competitive interactions between *Fucus spiralis* L. and *F. vesiculosus* L. (Fucales, Phaeophyta). *Hydrobiologia* 204/205, 205–209.
- Chapman, M.G., Underwood, A.J., 1998. Inconsistency and variation in the development of rocky intertidal algal assemblages. *J. Exp. Mar. Biol. Ecol.* 224, 265–289.
- Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* 18, 117–143.
- Commito, J.A., Currier, C.A., Kane, L.R., Reinsel, K.A., Ulm, I.M., 1995. Dispersal dynamics of the bivalve *Gemma gemma* in a patchy environment. *Ecol. Monogr.* 65, 1–20.
- Connolly, S.R., Menge, B.A., Roughgarden, J., 2001. A latitudinal gradient in recruitment of intertidal invertebrates in the northeast Pacific Ocean. *Ecology* 82, 1799–1813.
- Dayton, P.K., 1975. Experimental studies of algal canopy interactions in a sea otter-dominated kelp community at Amchitka Island, Alaska. *Fish. Bull. U. S. A.* 73, 230–237.
- Dayton, P.K., 1985. Ecology of kelp communities. *Ann. Rev. Ecol. Syst.* 16, 215–245.
- Dayton, P.K., Tegner, M.J., 1984. The importance of scale in community ecology: a kelp forest example with terrestrial analogs. In: Price, P.W., Slobodchikoff, C.N., Gand, W.S. (Eds.), *A New Ecology: Novel Approaches to Interactive Systems*. Wiley, New York, pp. 457–481.
- Dayton, P.K., Currie, V., Gerrodette, T., Keller, B.D., Rosenthal, R., Ven Tresca, D., 1984. Patch dynamics and stability of some California kelp communities. *Ecol. Monogr.* 54, 253–289.
- Dayton, P.K., Tegner, M.J., Parnell, P.E., Edwards, P.B., 1992. Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecol. Monogr.* 62, 421–445.
- Dayton, P.K., Tegner, M.J., Edwards, P.B., Riser, K.L., 1999. Temporal and spatial scales of kelp demography: the role of oceanographic climate. *Ecol. Monogr.* 69, 219–250.
- den Boer, P.J., 1968. Spreading of risk and stabilization of animal numbers. *Acta Biotheor.* 18, 165–194.
- Dethier, M.N., Graham, E.S., Cohen, S., Tear, L.M., 1993. Visual versus random-point percent cover estimations: “objective” is not always better. *Mar. Ecol. Prog. Ser.* 96, 93–100.
- Díez, I., Secilla, A., Santolaria, A., Gorostiaga, J.M., 1999. Phytobenthic intertidal community structure along an environmental pollution gradient. *Mar. Pollut. Bull.* 38, 463–472.
- Farnsworth, E.J., Ellison, A.M., 1996. Scale-dependent spatial and temporal variability in biogeography of mangrove root epibiotic communities. *Ecol. Monogr.* 66, 45–66.
- Field, J.C., Clarke, K.R., Warwick, R.M., 1982. A practical strategy for analysing multispecies distribution patterns. *Mar. Ecol. Prog. Ser.* 8, 37–52.
- Fraschetti, S., Bianchi, C.N., Terlizzi, A., Fanelli, G., Morri, C., Boero, F., 2001. Spatial variability and human disturbance in shallow subtidal hard substrate assemblages: a regional approach. *Mar. Ecol. Prog. Ser.* 212, 1–12.
- Gaines, S.D., Brown, S., Roughgarden, J., 1985. Spatial variation in larval concentration as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. *Oecologia* 67, 267–272.

- Gaston, K.J., McArdle, B.H., 1993. Measurement of variation in the size of populations in space and time: some points of clarification. *Oikos* 68, 357–360.
- Grosberg, R.K., 1982. Intertidal zonation of barnacles: the influence of planktonic zonation of larvae on vertical distribution of adults. *Ecology* 63, 894–899.
- Hoffman, L., Clarisse, S., Detienne, X., Goffart, A., Renard, R., Demoulin, V., 1988. Evolution of the populations of *Cystoseira balearica* (Phaeophyceae) and epiphytic Bangiophyceae in the Bay of Calvi (Corsica) in the last eight years. *Bull. Soc. R. Sci. Liège* 57, 263–273.
- Holling, C.S., 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecol. Monogr.* 62, 447–502.
- Hutchinson, N., Williams, G.A., 2001. Spatio-temporal variation in recruitment on a seasonal, tropical rocky shore: the importance of local versus non-local processes. *Mar. Ecol. Prog. Ser.* 215, 57–68.
- Johnson, C.R., Mann, K.H., 1988. Diversity, patterns of adaptation, and stability of Nova Scotian kelp beds. *Ecol. Monogr.* 58, 129–154.
- Kennelly, S.J., Underwood, A.J., 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.
- Konar, B., 2000. Limited effects of a keystone species: trends of sea otters and kelp forests at the Semichi Islands, Alaska. *Mar. Ecol. Prog. Ser.* 199, 271–280.
- Krönke, I., Dippner, J.W., Heyen, H., Zeiss, B., 1998. Long-term changes in macrofaunal communities off Nordeney (East Frisia, Germany) in relation to climate variability. *Mar. Ecol. Prog. Ser.* 167, 25–36.
- Levin, S.A., 1992. The problem of pattern and scale in ecology. *Ecology* 73, 1943–1967.
- Littler, M.M., Murray, S.N., 1975. Impact of sewage on the distribution, abundance and community structure of rocky intertidal macro-organisms. *Mar. Biol.* 30, 277–291.
- Mac Arthur, R.H., Wilson, E.O., 1967. The theory of island biogeography. Monographs in Population Biology. Princeton Univ. Press, Princeton, NJ, USA.
- Menconi, M., Benedetti-Cecchi, L., Cinelli, F., 1999. Spatial and temporal variability in the distribution of algae and invertebrates on rocky shores in the northwest Mediterranean. *J. Exp. Mar. Biol. Ecol.* 233, 1–23.
- Morrisey, D.J., Howitt, L., Underwood, A.J., Stark, J.S., 1992. Spatial variation in soft-sediment benthos. *Mar. Ecol. Prog. Ser.* 81, 197–204.
- Pineda, J., 1994. Spatial and temporal patterns in barnacle settlement rate along a southern California rocky shore. *Mar. Ecol. Prog. Ser.* 107, 125–138.
- Raimondi, P.T., 1988. Rock type affects settlement, recruitment, and zonation of the barnacle *Chthamalus anisopoma* Pilsbury. *J. Exp. Mar. Biol. Ecol.* 123, 253–267.
- Raimondi, P.T., 1990. Patterns, mechanisms, consequences of variability in settlement and recruitment of an intertidal barnacle. *Ecol. Monogr.* 60, 283–309.
- Rodríguez-Prieto, C., Polo, L., 1996. Effects of sewage pollution in the structure and dynamics of the community of *Cystoseira mediterranea* (Fucales, Phaeophyceae). *Sci. Mar.* 60, 253–263.
- Santelices, B., Ojeda, F.P., 1984. Population dynamics of coastal forests of *Macrocystis pyrifera* in Puerto Toro, Isla Navarino, Southern Chile. *Mar. Ecol., Prog. Ser.* 14, 175–183.
- Schiel, D.R., Foster, M.S., 1986. The structure of subtidal algal stands in temperate waters. *Oceanogr. Mar. Biol. Ann. Rev.* 24, 265–307.
- Schneider, D.C., 1994. Quantitative Ecology: Spatial and Temporal Scaling. Academic Press, San Diego, USA.
- Seapy, R.R., Littler, M.M., 1982. Population and species diversity fluctuations in a rocky intertidal community relative to severe aerial exposure and sediment burial. *Mar. Biol.* 71, 87–96.
- Searle, S.R., Casella, G., McCulloch, C.E., 1992. Variance Components. Wiley, New York.
- Smith, S.V., Buddemeier, R.W., 1992. Global change and coral reef ecosystems. *Ann. Rev. Ecol. Syst.* 23, 89–118.
- Sol, D., 2000. Are islands more susceptible to be invaded than continents? Birds say no. *Ecography* 23, 687–692.
- Southward, A.J., 1991. Forty years of changes in species composition and population density of barnacles on a rocky shore near Plymouth. *J. Mar. Biol. Assoc. UK* 71, 495–513.
- Thom, R.M., 1980. A gradient in benthic intertidal algal assemblages along the southern California coast. *J. Phycol.* 16, 102–108.
- Thrush, S.F., Hewitt, J.E., Cummings, V.J., Green, M.O., Funnell, G.A., Wilkinson, M.R., 2000. The generality of field experiments: interactions between local and broad-scale processes. *Ecology* 81, 399–415.

- Underwood, A.J., 1985. Physical factors and biological interactions: the necessity and nature of ecological experiments. In: Moore, P.G., Seed, R. (Eds.), *The Ecology of Rocky Coasts*. Hodder and Stoughton, London, pp. 372–390.
- Underwood, A.J., 1991. The logic of ecological experiments: a case history from studies of the distribution of macro-algae on rocky intertidal shores. *J. Mar. Biol. Assoc. UK* 71, 841–866.
- Underwood, A.J., 1996. Spatial patterns of variance in density of intertidal populations. In: Floyd, R.B., Shepard, A.W., De Barro, P.J. (Eds.), *Frontiers of Population Ecology*. CSIRO Publishing, Melbourne, Australia, pp. 369–389.
- Underwood, A.J., 1997. *Experiments in Ecology. Their Logical Design and Interpretation Using Analysis of Variance*. Cambridge Univ. Press, Cambridge, UK.
- Underwood, A.J., Chapman, M.G., 1996. Scales of spatial patterns of distribution of intertidal invertebrates. *Oecologia* 107, 212–224.
- Vogt, H., Schramm, W., 1991. Conspicuous decline of *Fucus* in Kiel Bay (Western Baltic): what are the causes? *Mar. Ecol. Prog. Ser.* 69, 189–194.
- Wiens, J.A., Stenseth, N.C., Van Horne, B., Ims, R.A., 1993. Ecological mechanisms and landscape ecology. *Oikos* 66, 369–380.
- Williams, G.A., Davies, M.S., Nagarkar, S., 2000. Primary succession on a seasonal tropical rocky shore: the relative roles of spatial heterogeneity and herbivory. *Mar. Ecol. Prog. Ser.* 203, 81–94.
- Winer, B.J., Brown, D.R., Michelis, K.M., 1991. *Statistical Principles in Experimental Design*, 3rd ed. McGraw-Hill, USA.
- Wu, J., Loucks, O.L., 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. *Q. Rev. Biol.* 70, 439–466.