Variability of Mediterranean coralligenous assemblages subject to local variation in sediment deposition

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Abstract

This study tested whether the development of coralligenous assemblages on horizontal and vertical surfaces differed between localities of high and low sediment deposition. The development and structure of these assemblages varied in predictable ways according to the level of sediment deposition. These differences were largely independent of the orientation of substratum. Turfs were more extensive in areas of high sediment deposition while erect and encrusting algae were most extensive in areas of low sediment deposition. Encrusting invertebrates characterised vertical surfaces and were most extensive in areas of high sediment deposition. These results are consistent with studies from other temperate regions of the globe, suggesting that effects of sedimentation on temperate coasts are substantial and widespread.

Keywords: Sedimentation; Coralligenous assemblages; Deep sublittoral; Substrate orientation; Temporal fluctuations; Mediterranean Sea

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1. Introduction

Rates of sedimentation have increased over the past few decades in many coastal marine areas, representing a potential threat to littoral communities (Airoldi, 2003, & references therein). Sedimentation in littoral systems is linked to terrestrial sources and can be affected by human activities that have historically altered the transport of suspended sediments and increased the erosion on watersheds (Valiela, 1995). The loss of soil due to overuse of land or deforestation has been recently accelerated, producing a worldwide increase of water turbidity and sedimentation load in coastal areas (Airoldi, 2003, & references therein).

Although less investigated than other physical factors, sedimentation is potentially one of the major factors influencing structure, biomass and metabolism of marine benthic communities. Deterioration and lost of tropical coral communities have been observed following increased sediment loads (Rogers, 1983, 1990; Wittenberger & Hunte, 1992). Seagrass growth and stability are influenced by variations of sediment deposition (Blanc & Jeudy de Grissac, 1989) and the structure of temperate rocky assemblages varies in relation to sedimentation rates (Airoldi, 1998; Gorgula & Connell, 2004; Kendrick, 1991; McQuaid & Dower, 1990). Moreover, high rates of sediment deposition can be a threat to the overall richness and diversity of the communities (Airoldi & Cinelli, 1997).

Sedimentation may affect benthic organisms through several mechanisms. Sediments may cover sessile organisms clogging filtering apparata and inhibiting recruitment, growth and metabolic processes. Resuspended sediments may increase water turbidity, limiting algal production. Moreover, severe burial and scouring may cause death and removal of sessile organisms (Airoldi, 2003; Irving & Connell, 2002a).

Most studies on sedimentation in temperate seas have been carried out in intertidal habitats (D’Antonio, 1986; Daly & Mathieson, 1977; Littler, Martz, & Littler, 1983; Seapy & Littler, 1982; Stewart, 1983), while relatively few concerned shallow subtidal assemblages (Airoldi, 1998, 2000a; Eriksson & Johansson, 2003; Irving & Connell, 2002a, 2002b). Little is known about the effects of sedimentation on deep (>30 m) littoral communities.

In the Mediterranean Sea, the deep littoral systems (between 25–30 and 150–200 m) are colonised by assemblages dominated by calcareous organisms, generally referred to as “coralligenous” (Pèrès & Picard, 1964; Sarà & Pulitser-Finali, 1970). Coralligenous assemblages develop on rocky shores and on sand planes in relatively constant conditions of temperature, currents and salinity and wherever irradiance is reduced between 2–3% and 0–0.5% of the surface irradiance (Garrabou & Ballesteros, 2000). Coralligenous is a typical biotope of the lower sublittoral, which consist of blocks of organic concretionary material, originated principally by the dead thalli of crustose coralline algae (Lithophyllum spp.) and secondarily by bio-constructor animals as polychaetes, bryozoans and gorgonians. These blocks constitute a hard substratum on which highly diverse assemblages develop (Cocito, Ferdeghini, & Sgorbini, 2001; Hong, 1982; Laborel, 1961; Labier, 1966; Lüning, 1990). Thus, coralligenous assemblages are characterized by high richness, biomass and production, with values comparable to tropical reef assemblages, so that it can be considered one
of the most important and characteristic assemblages of the Mediterranean Sea (Bianchi, 2001).

Despite its complexity, the coralligenous system is considered fragile, as its persistence is related to the maintenance of peculiar biotic and abiotic factors (Hong, 1983). As in other ecosystems, the increase of turbidity, burial and sediment deposition may represent a threat to coralligenous assemblages. In shallow sublittoral habitats, correlative and manipulative studies showed that disturbance related to sediment may favour the development of species resistant to burial or with opportunistic life-histories (Airoldi, 2000a, 2003; Airoldi, Rindi, & Cinelli, 1995). Similar effects have been described for littoral sand planes, where increased sediment loads led to regression of the lower limit of coralligenous assemblages, to the disappearance of several organisms and to changes in the community structure (Bourcier, 1986). On the contrary, little is known about sediment effects on rocky coralligenous assemblages, even though they have been considered as a factor influencing the spatial and temporal variability (Morganti, Cocito, & Sgorbini, 2001).

In this paper, we propose that coralligenous assemblages differ between areas characterized by different sedimentation conditions. Moreover, we propose that differences between assemblages are linked to substrate inclination, horizontal substrata being more affected by sediment deposition. To test these hypotheses, coralligenous assemblages of a rocky bank were studied during 1-year period through photographic samplings. A hierarchical sampling design was used to test differences in spatial and temporal variability between assemblages developed on horizontal and vertical substrata in areas characterised by different turbidity and sediment deposition. A combination of univariate and multivariate analysis was used to evaluate variability at different spatial scales within each interaction between sedimentation level and substrate inclination.

2. Materials and methods

2.1. Study area

The research was carried out on Vada Shoals, a bank situated about 8 km off the Tuscan coast (Fig. 1). This bank consists of a wide sandstone platform that extends 80 km² seaward, from 8 m to about 50 m in depth. Up to 25 m, the bottom is covered by meadows of the phanerogam Posidonia oceanica (L.) Delile, while coralligenous assemblages characterize the deeper part of the bank. The bottoms surrounding the bank consist of organogenous sand and rhodolith communities.

Two areas with different average levels of water turbidity were identified during a 10-month (from February to December 2001) survey that monitored the water column through a multiparametric probe (Ocean Seven 316) (Fig. 2). In each area, three replicates random measures were collected for each of six times during the survey period. The turbidity was indicated as NTU (nephelometric turbidity unit). The probable causes of water turbidity in the area can be linked to the contribution of
sediment transported by currents from the coast, where two small rivers flow into the sea (Fig. 1).

2.2. Sampling design

Sampling of coralligenous assemblages established at 32–35 m depth was carried out on five random dates during March 2002–February 2003. Within each condition (high sedimentation vs. low sedimentation), two locations some km apart were randomly chosen (Fig. 1) with both horizontal and vertical substrata interspersed in

![Fig. 1. Vada Shoals with sampling locations. Grey stars indicate locations characterized by low sedimentation while black stars indicate locations characterized by high sedimentation. Arrows indicate the mouths of the rivers.](image)

![Fig. 2. Turbidity level (mean ± SE) in high (H) and low (L) water turbidity areas of Vada Shoals measured at 28 m depth.](image)
each location. For each type of substratum inclination (horizontal vs. vertical), two sites were randomly chosen within each location and the percent cover of benthic organisms was sampled through photographic methods within each site ($n = 8$).

2.3. Assessment of sediment

The amount of sediment deposited over the coralligenous assemblages at each location was quantified by sucking all sediments accumulated in sampling units of $25 \times 20$ cm of horizontal substrata by using a suction pump. In each location, sediment was collected from three sampling units randomly chosen at each of five sampling dates. The material collected in nylon stockings was retained on ignited and pre-weighed GF/F glass microfiber filters (0.7 μm). The material was rinsed with distilled water to remove salts and dried to constant weight ($60^\circ$C for 24 h) before weighing on a Ohaus balance to a precision of $10^{-4}$ g in the presence of silica gel (Airoldi, Fabiano, & Cinelli, 1996). The values obtained have been transformed in g m$^{-2}$. This method was used to compare sediment deposition between areas characterized by different condition. Although this method cannot be considered suitable to quantify the absolute sediment abundance because of the loss of the finest part, it may be effective to evaluate relative spatial and temporal differences of deposited sediments.

Quantitative data of sediment were analysed by three way ANOVA with date (five levels) as random factor, condition (two levels) as fixed and orthogonal factor and locations (two levels) as random and nested in condition. Cochran’s $C$-test was utilised before each analyses to check for homogeneity of variance (Underwood, 1997).

2.4. Collection and analysis of data

Sampling was carried out by Scuba divers using a Nikonos-V camera with 35 mm lens fitted with an additional lens and with a framer (Pronzato, 1997), able to photograph surfaces of 240 cm$^2$ (Acunto, Balata, & Cinelli, 2001). Slides were projected onto a grid of 96 small squares. Cover of each taxon ($X$) was considered as the number of squares filled in the grid by the taxon and expressed as percentage through the formula $\frac{X}{96} \times 100$. An arbitrary 0.2% was attributed to the organisms with a cover smaller than 1/2 square (Dethier, Graham, Cohen, & Tear, 1993; Ferdeghini, Acunto, Cocito, & Cinelli, 2000). Algae were divided into encrusting, turf and erect species, while phyla were considered for sessile animals. Some taxa easily identified to species level by photographs were not grouped into vegetation layer or phyla and considered separately in the multivariate analysis.

The differences in percent cover of sponges, anthozoans, bryozoans and encrusting, turf and erect algae were analysed using five-way analyses of variance (ANO-VAs) with date (five levels) as random factor, condition (two levels) as orthogonal and fixed factor, location (two levels) as random factor nested in condition, inclination (two levels: vertical substrata vs. horizontal substrata) as orthogonal and fixed factor and site (two levels) as random factor nested in the interaction location (condition) $\times$ inclination $\times$ date. Cochran’s $C$-test was utilised before each analyses to
check for homogeneity of variance and data were transformed when necessary (Underwood, 1997). The non-parametric multivariate analysis of variance (NP-MANOVA; Anderson, 2001) was used to test the null hypothesis that coralligenous assemblages were not significantly influenced by the factors condition, inclination of the substrata, temporal and spatial variability and moreover by the interactions between these factors. The factors and the levels utilized for this analysis were the same adopted in the univariate analysis. The mean square (MS) of the interaction date × location was used as denominator for the sources of variability date, location and date × condition; the permutable units for these tests were the 20 combinations among date and location. The MS of the factor location was used as denominator for the sources of variability condition; for this test the permutable units were the four locations. The MS of the interaction location × inclination was utilized as denominator for the sources of variability inclination and condition × inclination; the permutable units for these tests were the eight combinations among locations and inclinations.

The MS of the factor site was used as denominator for the sources of variability date × location and date × location × inclination; the permutable units for these tests were the 80 sites. The MS of the interaction date × location × inclination was used as denominator for the sources of variability date × inclination, location × inclination and date × condition × inclination; the permutable units for these tests were the two sites for each combination of date, location and inclination (total number of permutable units = 40). Finally, the factor site was tested over the residual MS, using the individual observations as permutable units. Bray–Curtis measures of dissimilarity (Bray & Curtis, 1957) were used to calculate a matrix of distances between each pair of samples. Data of percent cover of organisms were square root transformed before calculation of Bray–Curtis coefficients. A two-dimensional MDS (multidimensional scaling) was used for a graphical representation of the data.

3. Results

3.1. Sediments

Throughout the study period, the dry weight of sediment deposited on horizontal substrata was higher in locations sited inside the area characterised by higher water turbidity, (Fig. 3). In high sedimentation area, values ranged between 44.3 and 130.9 g dry weight/m², while in low sedimentation area from 6.3 to 49.7 g dry weight/m². ANOVA detected as significant the interaction between condition and date (Table 1). The Snk test showed that differences between the areas with different conditions were significant throughout the study period.

These results indicate a close relation between the level of turbidity and the amount of sediment on the deep sublittoral bottoms in the study area.
3.2. Assemblages

In the low sedimentation area encrusting algae dominated the coralligenous assemblages, erect and turf algae were abundant mostly on horizontal substrata, while sessile animals showed high covers on vertical substrata.

Encrusting algae mostly consisted of encrusting Corallinaceae and species of the genus Peyssonnelia. The Phaeophyta Zanardinia typus (Nardo) G. Furnari and the Chlorophyta Palmophyllum crassum (Naccari) Rabenhorst were also present on horizontal and vertical substrata, respectively. Encrusting algae were abundant on both substrata; in the low sedimentation area, their cover was generally higher than 50%, while in the high water turbidity area values ranged between 20% and 30% (Fig. 4(a)).

The most common species in the turfs were the Rhodophyta Womersleyella setacea (Hollenberg) R.E. Norris, Rodriguezella strafforeloii F. Schmitz, Feldmannophycus rayssiae (Feldmann & Feldmann-Mazoyer) Augier & Boudouresque, Eupogodon spp. and the Chlorophyta Pseudochlorodesmis furcellata (Zanardini) Børgesen. Turfs were persistent during all the study period with higher abundance on horizontal substrate and in the high sedimentation area, where the percent cover showed values around 50% (Fig. 4(b)).
Among the erect algae were widely distributed the Rhodophyta *Meredithia microphylla* (J. Agardh) J. Agardh, *Osmundaea pelagosa* (Schiffner) F.W. Nam and the Chlorophyta *Flabellia petiolata* (Turra) Nizamuddin. The erect layer showed a higher cover in the low sedimentation area and in the first three dates, corresponding to the warmer months. In the first period, the percent cover was greater on horizontal
substrata than on the vertical ones, but this pattern was not consistent in the two last sampling dates (Fig. 4(c)).

_Scyzzomavella_ sp. was the most common encrusting bryozoan in the study area, while among the erect forms were present _Myriapora truncata_ (Pallas), _Pentapora fascialis_ (Pallas), and _Sertella_ sp. The percent cover of bryozoans was higher in high sedimentation area and on vertical substrata (Fig. 5(a)).

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**Fig. 5.** Mean percentage cover (±SE) of the main sessile animals in the coralligenous assemblages of Vada Shoals on horizontal (h) and vertical (v) substrata and in high (H) and low (L) sedimentation areas.
Sponges were mostly distributed on vertical substrata and in the high sedimentation area (Fig. 5(b)).

Anthozoans had always low cover and generally characterized the vertical substrata (Fig. 5(c)), mostly with *Parazoanthus axinellae* (Schmidt) and *Leptosammia pruvoti* Lacaze-Duthiers; *Cladocora caespitosa* (Linneus) was the only anthozoan distributed on the horizontal substrata.

ANOVA detected as significant differences in percent cover of turf, erect and encrusting algae between areas characterised by different conditions (Table 2). Turfs were more abundant in high sedimentation area, while erect and encrusting forms had high cover in low sedimentation area. Turf and erect algae were more abundant on horizontal than vertical substrata, but the significance depended on the date of sampling for turf and on date and location for erect algae. ANOVA detected as significant also the interaction between condition and inclination for the percent cover of bryozoans and sponges (Table 2), which were more abundant on vertical substrata and in the high sedimentation area. Anthozoans had a significantly higher cover on vertical than horizontal substrata. The percent cover of sponges, bryozoans, turf, erect and encrusting algae showed a significant interaction between date and location. Spatial variability at small scales was generally high for all the organisms, as showed by the significance of the site factor.

MDS ordination showed in all the five dates, a clear distinction between the two conditions (Fig. 6). NPMANOVA detected significant differences in the structure of assemblages in relation to sedimentation, inclination and date (Table 3). In agreement with the univariate analysis, the multivariate analysis also indicated heterogeneity in the assemblages at the scale of both location and site.

4. Discussion

Results of this work showed that the structure of coralligenous assemblages of Vada Bank differed between areas characterized by different water turbidity and sediment deposition. It is interesting to underline that these differences were significant on both the substrata and they persisted throughout the study period independently of the changes in the amount of sediment deposited. Horizontal substrata may be more affected by sedimentation than vertical substrata because the deposition and accumulation of sediment is greater on these surfaces (Cocito, Bedulli, & Sgorbini, 2002). In the present work, sediment sampling was conducted in order to detect differences in sediment deposits between the two areas characterized by different conditions and between locations in each area. Thus, data are not suitable to be linked to patterns of assemblages and no information is available about sediments on vertical substrata. However, the absence of interactions between substratum inclination and sedimentation condition for algae, that are the main component of these assemblages, suggests that sedimentation-related mechanisms other than deposition, such as burial and changes to water turbidity, may also be important for the assemblages sampled. By this descriptive work, it is impossible to separate the main mechanisms through which sediment could influence coralligenous assemblages. Sediment
Table 2
Results of the five-way ANOVA on percent cover of the main taxa and vegetation layers identified

<table>
<thead>
<tr>
<th>Source</th>
<th>Encrusting algae</th>
<th>Turf algae</th>
<th>Erect algae</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>MS</td>
<td>F</td>
<td>P</td>
</tr>
<tr>
<td>Date = D</td>
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<td>3159.83</td>
<td>3.66</td>
</tr>
<tr>
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<td>217028.14</td>
<td>32.79</td>
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<td>6617.26</td>
<td>7.68</td>
</tr>
<tr>
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<td>6445.89</td>
<td>1.71</td>
</tr>
<tr>
<td>Site (D × L(C) × I)</td>
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<td>274.15</td>
<td>1.69</td>
</tr>
<tr>
<td>D × C</td>
<td>4</td>
<td>1400.17</td>
<td>1.63</td>
</tr>
<tr>
<td>D × L(C)</td>
<td>8</td>
<td>861.55</td>
<td>3.14</td>
</tr>
<tr>
<td>D × I</td>
<td>4</td>
<td>534.52</td>
<td>1.01</td>
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<tr>
<td>C × I</td>
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<td>450.74</td>
<td>0.12</td>
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<td>L(C) × I</td>
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<td>3752.55</td>
<td>7.13</td>
</tr>
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<tr>
<td>Total</td>
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<td></td>
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<tr>
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<td>0.0503 ns</td>
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<tr>
<td>Transformation</td>
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</tr>
</tbody>
</table>

|                                | Anthozoans | Bryozoaons | Sponges    |
|                                | MS         | F          | P           | MS         | F          | P           | MS         | F          | P           |
| Date = D                       | 4          | 2.04       | 0.46       | >0.70       | 1.34       | 1.21       | >0.30       | 4.30       | 0.73       | >0.50       |
| Condition = C                  | 1          | 0.01       | 0.04       | >0.80       | 2.97       | 8.33       | <0.05       | 79.44      | 6.07       | >0.10       |
| Location (C) = L(C)            | 2          | 1.86       | 0.42       | >0.60       | 0.22       | 0.20       | >0.80       | 13.08      | 2.22       | >0.10       |
| Inclination ≈ I                | 1          | 41.66      | 30.62      | <0.01       | 52.82      | 64.97      | <0.05       | 125.86     | 43.85      | <0.01       |
| Site (D × L(C) × I)            | 40         | 2.86       | 2.38       | <0.01       | 0.43       | 1.51       | <0.05       | 2.60       | 2.62       | <0.01       |
| D × C                          | 4          | 0.23       | 0.05       | >0.90       | 0.35       | 0.32       | >0.80       | 1.45       | 0.24       | >0.90       |
| D × L(C)                       | 8          | 4.40       | 1.53       | >0.15       | 1.10       | 2.54       | <0.05       | 5.89       | 2.26       | <0.05       |
| D × I                          | 4          | 1.36       | 0.40       | >0.80       | 0.34       | 0.51       | >0.70       | 2.87       | 1.94       | >0.10       |
| C × I                          | 1          | 1.54       | 0.39       | >0.50       | 2.69       | 18.23      | <0.05       | 11.52      | 32.89      | <0.01       |
| L(C) × I                       | 2          | 3.88       | 1.14       | >0.30       | 0.81       | 1.20       | >0.30       | 2.06       | 1.39       | >0.30       |
| D × C × I                      | 4          | 2.15       | 0.63       | >0.60       | 0.14       | 0.21       | >0.90       | 0.35       | 0.23       | >0.90       |

(continued on next page)
Table 2 (continued)

<table>
<thead>
<tr>
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<th>Anthozoans</th>
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<td>3.37</td>
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Significant values are written in bold.
deposition and water turbidity may combine to affect benthic communities and their effects may be different in relation to the morphological and physiological characteristics of dominant species (Irving & Connell, 2002a), contributing to make it difficult the interplay of observed patterns. A synergistic effect between sedimentation and shading could be involved determining significant differences between assemblages influenced by different sediment conditions both on horizontal and on vertical substrata.

In the high sedimentation area, turfs were dominant and sessile animals were also abundant on vertical substrata, while erect and encrusting algae had high cover in the low sedimentation area. These patterns are in agreement with previous studies,

Fig. 6. nMDS plot showing at the five sampling dates the dissimilarity among centroids of sites on vertical (v) and horizontal (h) substrata and in high (H) and low (L) sedimentation areas.
carried out in shallow assemblages, that showed shifts in community composition among zones with different sedimentation rates (Airoldi & Cinelli, 1997; Irving & Connell, 2002a; Piazzi & Cinelli, 2001). In agreement with Irving and Connell (2002a), sedimentation can affect the structure of communities both functionally, damaging photosynthetic organisms, and morphologically, damaging differently the organisms according to their form. Airoldi (2000a) considered the importance of life history of algae for their adaptation to disturbance caused by sedimentation. Turf algae appeared more resistant to high sedimentation than erect and encrusting forms (Gorgula & Connell, 2004). In shallow habitats, sediment scour and burial can remove organisms during storms and sediment deposition can limit the availability of substrate for spore settlement. Turf species reproduce vegetatively and can reconstitute populations from fragments of prostrate thalli quicker than species reproducing by spores and independently from the period of the year in which the perturbation occurs (Airoldi, 2000a; Irving & Connell, 2002b; Sousa, Schroeter, & Gaines, 1981). Moreover, turfs can trap sediments, and this could enhance their competitiveness, facilitating the pre-emption of substrate and preventing grazing (D’Antonio, 1986; Kendrick, 1991; Stewart, 1983). On the contrary, erect and encrusting species, that reproduce sexually, could be affected by sediment deposition and by competition with turf: in fact, the contemporaneous presence of deposited sediments and turfs can prevent spore settlement (Airoldi, 2000a, 2000b; Chapman & Fletcher, 2002) and, moreover, this effect can increase with depth (Eriksson & Johansson, 2003). Competition among macroalgae together with disturbance and physical stress are considered two fundamental processes to determine the patterns of distribution and abundance of algal species (Paine, 1990). In coralligenous habitats, these mechanisms could be also involved, although scouring and burial could have lower importance than in shallow water and sediment effects could be

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<th>Source</th>
<th>df</th>
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</tr>
<tr>
<td>D × L(C)</td>
<td>8</td>
<td>13121.06</td>
<td>1640.16</td>
<td>2.646</td>
<td>&lt;0.001</td>
<td>Site (D × L(C) × I)</td>
</tr>
<tr>
<td>D × I</td>
<td>4</td>
<td>6717.00</td>
<td>1679.19</td>
<td>1.406</td>
<td>&gt;0.250</td>
<td>D × L(C) × I</td>
</tr>
<tr>
<td>C × I</td>
<td>1</td>
<td>3900.78</td>
<td>3900.78</td>
<td>1.059</td>
<td>&gt;0.400</td>
<td>L(C) × I</td>
</tr>
<tr>
<td>L(C) × I</td>
<td>2</td>
<td>7364.59</td>
<td>3682.29</td>
<td>3.083</td>
<td>&lt;0.040</td>
<td>D × L(C) × I</td>
</tr>
<tr>
<td>D × C × I</td>
<td>4</td>
<td>3675.91</td>
<td>919.54</td>
<td>0.759</td>
<td>&gt;0.600</td>
<td>D × L(C) × I</td>
</tr>
<tr>
<td>D × L(C) × I</td>
<td>8</td>
<td>9553.81</td>
<td>1194.20</td>
<td>1.927</td>
<td>&lt;0.010</td>
<td>Site (D × L(C) × I)</td>
</tr>
<tr>
<td>Residual = R</td>
<td>560</td>
<td>254005.90</td>
<td>453.61</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>639</td>
<td>560748.24</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Transformation: Square root

Bold type indicates a significant effect.
principally linked to deposition and decreasing of light incidence. Appropriate studies are needed to investigate how coralligenous assemblages are affected by sediment disturbance.

In the present study sessile animals, especially sponges and bryozoans, showed a higher cover in the high sedimentation area, particularly on vertical substrata. A possible explanation is that the morphological aspect could be important also for animals. In fact animals are more adapted, than algae to low light conditions caused by suspended sediments. Thus, forms resistant to sediment deposition could have a higher competitiveness than algae in habitats influenced by sedimentation (Irving & Connell, 2002a).

The studied assemblage was mostly characterised by algae both on horizontal and vertical substrata. In low sedimentation areas, encrusting algae dominated everywhere, while sessile animals were more abundant on vertical substrata and erect and turf algae were more developed on horizontal substrata.

The abundance of turf and erect algae changed throughout the year resulting in the interaction between date and inclination for turf algae and in the interaction date \( \times \) location (condition) \( \times \) inclined for erect algae. These results suggest that temporal variability may be important also in coralligenous communities. This pattern is in agreement with previous observations (Abbiati, Virgilio, & Querci, 1996; Piazzi, Balata, Pertusati, & Cinelli, 2004) and represents an interesting topic of further investigations. A higher temporal variability of horizontal assemblages compared to the vertical ones was already described for shallower habitats and attributed to seasonal cycles of photophilic organisms (Piazzi, Pardi, Balata, Cecchi, & Cinelli, 2002). In the studied assemblages changes in abundance of erect algae could be related to life cycles of the main species. This finding indicate that coralligenous assemblages, normally considered steadier than shallow rocky assemblages, is subjected to seasonal modification when algal component is dominant.

Multivariate analysis showed significant differences between assemblages developed on horizontal and vertical substrata; univariata analysis indicated that differences were principally linked to sessile animals. A higher abundance of animals on vertical substrata is common for shallow water assemblages both in the Mediterranean and other seas (Baynes, 1999; Glasby, 2000). This work confirms this pattern also for deep assemblages. Light is considered the main factor to determine differences between assemblages on horizontal and vertical substrata (Irving & Connell, 2002a). In fact, larvae of animals are more attracted by shade (Dirnberg, 1993; Glasby & Connell, 2001; Saunders & Connell, 2001), while algal recruitment and development are higher on horizontal bottoms, where light irradiance is higher (Goldberg & Forster, 2002). Shade could operate also indirectly influencing biological interaction by limiting the growth of dominant algae. Sponge communities preferred vertical and shaded substrata, probably being limited by solar radiation and by the growth of competitive algae (Pansini, Morri, & Bianchi, 2000). An analogous situation has been observed for Bryozoans and solitary ascidian (Glasby, 1999).

The studied assemblages showed a high variability at small and medium scales. This finding is in agreement with the one observed by previous studies on coralligenous assemblages and attributed to a patch distribution of organisms linked both to
the heterogeneity of substrate and to the interactions among sessile organisms (Acunto et al., 2001; Ferdeghini et al., 2000). Small scale topographical heterogeneity is considered responsible of patch distribution, influencing recruitment, offering suitable refuges and creating microhabitats with different physical conditions (Archambault & Bourget, 1996; Lapoint & Bourget, 1999; Walters & Wethey, 1996). In coralligenous assemblages competition for space represents one of the main processes determining patterns of distribution. In fact, crustose organisms that characterize this system compete intensely for substratum because limited to use space in only two dimensions (Carpenter, 1990) and this process could concur to increase patchiness. Moreover, patch distribution in algal assemblages seems to increase with depth, mostly linked to light attenuation but also to other physical factors (Schiel & Foster, 1986). As a result of the present and other studies (Piazzi et al., 2002, 2004), coralligenous assemblages seems to have a large-scale homogeneity, resulting in a lack of significant differences between separated locations (Piazzi et al., 2004), while at small scale a high heterogeneity is always evident. This finding demonstrates that spatial variability is not scale independent also in coralligenous assemblages, such as in other marine habitats (Benedetti-Cecchi, 2001; Underwood & Chapman, 1996), allowing to optimize sampling designs for further studies.

The differences found in the present study between assemblages influenced by different water turbidity and sediment deposition suggest that the increase of sedimentation in the Mediterranean Sea could negatively affect also coralligenous rocky communities, such as already demonstrated in other habitats as deep sand bottoms and shallow rocky shores (Airoldi, 2003; Airoldi & Cinelli, 1997; Bourcier, 1986).

By this correlative work, it is impossible to conclude that differences between assemblages are linked only to sedimentation, as other factors could be involved, especially considering that the study locations with different conditions are necessarily segregated. However, it is right to suppose that sedimentation could influence the observed patterns, as the relationships between sediment deposition and abundance of dominant taxa were similar to those observed in manipulative experiments in shallow habitats. Moreover, results of the study are in agreement with observations of other authors suggesting the importance of sedimentation to affect the structure of coralligenous assemblages (Cocito et al., 2002; Morganti et al., 2001). Appropriate manipulative experiments are needed to identify cause/effect relationships.

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References


