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Coralligenous habitat: patterns of vertical distribution of macroalgal assemblages

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SUMMARY: The present study investigates patterns of distribution of macroalgal coralligenous assemblages in relation to depth and evaluates the role of different environmental conditions on these patterns. Two depths (30 and 40 m) were investigated off small islands and off continental coasts in order to select two different environmental conditions. Results showed differences between depths in the structure of assemblages around islands, while along the continental coasts these patterns were not evident. Moreover, differences between assemblages related to different environmental conditions were more evident in the shallower zone of distribution of the coralligenous habitat. This correlative study did not allow us to identify any cause-effect relationship, but patterns we detected agree with those of other studies, suggesting that alterations in the environmental conditions may be the cause of the decrease in differences among assemblages developing at different depths and may lead to a higher spatial homogenization and an impoverishment of the whole subtidal system.

Keyworks: coralligenous habitat, depth, disturbance, macroalgae, Mediterranean Sea.

RESUMEN: HÁBITAT CORALÍGENO: PATRONES DE DISTRIBUCIÓN VERTICAL DE CONJUNTOS DE MACROALGAS. – Este estudio investiga los patrones de distribución de las comunidades algales del hábitat coralígeno en relación a la profundidad y evalúa el papel de las diferentes condiciones ambientales en la formación de estos patrones. Se han muestreado dos profundidades (30 y 40 m) en pequeñas islas y en la costa continental. Los resultados muestran diferencias entre profundidades en la estructura de las comunidades entre islas, mientras que estas diferencias no son evidentes en el continente. Además las diferencias encontradas son más evidentes a 30 metros. Este estudio correlacional no nos permite establecer ninguna relación causa-efecto; sin embargo, los patrones detectados están de acuerdo con lo observado en otros trabajos, lo que sugiere que las alteraciones en las condiciones ambientales pueden ser la causa de la disminución de las diferencias entre comunidades distintas y pueden provocar una mayor homogeneidad espacial y un empobrecimiento de la zona sublitoral.

Palabras clave: hábitat coralígeno, profundidad, perturbación, macroalgas, mar Mediterráneo.

INTRODUCTION

Depth is one of the main causes of distribution in marine organisms (Vadas and Steneck, 1988; Garrabou *et al.*, 2002; Konar *et al.*, 2009; Terlizzi *et al.*, 2010). In fact, the main physical factors regulating life in marine systems, such as light, water movement, temperature, sedimentation and nutrient availability are depth-related (Pérès and Picard, 1964). In coastal habitats, other factors, such as the morphology of the bottom, physical and chemical characteristics of water and biotic interactions, can modify the vertical patterns of distribution (Underwood, 1992; Benedetti-Cecchi *et al.*, 2000; Glasby and Connel, 2001; Irving and Connel, 2002; Airoldi, 2003; Diez *et al.*, 2003; Dauer *et al.*, 2008). In this context, human activities can influence patterns of variability, amplifying these changes (Chapman *et al.*, 1995). This latter aspect is understudied, although it might furnish fundamental ecological information for understanding the spatial patterns in impact evaluations or monitoring surveys.

In the Mediterranean Sea, shallow subtidal rocky habitats are dominated by photophilous assemblages of



FIG. 1. – Values of turbidity (measured through a multiparametric probe) (a), transparency (measured through Secchi disc) (b), concentration of NH₄ (c) and NO₃ (d) obtained in two different surveys along the Tuscany coasts (mean±SE, n=8)

macroalgae mostly belonging to Ochrophyta (Gili and Ros, 1985; Balata and Piazzi, 2008), while the deep subtidal zone is characterized by peculiar assemblages associated with coralligenous habitats (sensu Ballesteros, 2006). This habitat consists of calcareous structures built by algae belonging to the family Corallinales and developing under reduced irradiance. Vertical distribution of coralligenous assemblages has not been suitably assessed, though several patterns have emerged from previous studies (Balata *et al.*, 2006). Moreover, although the effects of different kinds of disturbance on coralligenous assemblages have been investigated (Balata *et al.*, 2007a, 2007b; Piazzi *et al.*, 2007), there is no evidence of the influence of environmental conditions on vertical patterns.

The present study aimed to describe patterns of distribution of macroalgal coralligenous assemblages in relation to depth and to determine whether these patterns remain constant under different environmental conditions. The following hypotheses were tested: i) the structure of coralligenous assemblages differs between depths, and 2) patterns of vertical distribution change under different environmental conditions related to coast vs island habitats.

MATERIALS AND METHODS

The study was carried out in Tuscany, in the NW Mediterranean Sea, in summer 2008. Two depths (30 and 40 m) were investigated on horizontal rocky bottoms; we chose these depths because they can be considered, respectively, as the minimal and the maximal depth at which it is possible to find coralligenous

habitats on rocky substrate in the study area. In order to select two different environmental conditions, small islands and continental coasts were considered. In fact, small islands and continental coasts can generally differ in environmental conditions and levels of anthropogenic disturbance (Benedetti-Cecchi et al., 2003). In our study this model was based on data previously obtained by the monitoring survey carried out by AR-PAT (Environmental Agency of Tuscany) along the Tuscan coasts (Fig. 1). For each condition and depth, 4 sites (20 m²) several kilometres from each other were chosen (Fig. 2) and three replicate plots of 400 cm^2 were sampled at each site (Boudouresque 1971, 1973). All organisms were collected in each plot by scraping the substrate with a hammer and a chisel. Macroalgae were identified and the abundance of each species was expressed as percentage cover. Total percentage cover was calculated by summing the percentage cover of each species found in each plot. Taxonomic nomenclature follows Guiry and Nic Dhonncha (2009).

Data were analyzed by permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001) with a 3-way model with Depth (30 m vs. 40 m) and Condition (Island vs. Coast) as fixed and crossed factors, and Site (4 levels) as a random factor nested in the interaction Depth \times Condition. Bray-Curtis measures of dissimilarities in untransformed data were used to calculate a matrix of distances between pairs of samples. A pairwise test was used to discriminate among levels of significant factors. A SIMPER test (Clarke 1993) was used to determine species responsible for multivariate patterns. SIMPER tests analysed the comparisons between the levels of the Condition \times Depth



FIG. 2. - Map of the study area. Symbols indicate the sampling sites. Stars, small islands; triangles, continental coasts

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TABLE 1. –	Results of	PERMANOVA	analysis.	Significant	results
		are in bold.	-	-	

Source	df	MS	Pseudo-F	P(perm) Number of permutations	
Condition (C) Depth (D) C×D Site (C×D) Residual Total	1 1 12 32 47	11157 16254 6855 2408.2 549.84	4.6331 6.7495 2.8466 4.3798	0.002 0.001 0.024 0.001	999 999 999 999 999
Pairwise tests (C×D)		-30 m: -40 m: coast island	coast, island coast, island -30 m, -40 m -30 m, -40 m	0.002 0.205 0.181 0.001	

interaction that were significant in the pairwise tests (PERMANOVA).

A 2-dimensional nMDS (non-metric multidimensional scaling) based on centroids for replicate sites was used as a graphical representation of the data. Distances among centroids were obtained using principal coordinate axes from the original Bray-Curtis matrix.

Values of species richness and total percentage cover were analyzed by a 3-way ANOVA, utilizing the same factors and levels as those described for the multivariate analysis. Homogeneity of variances was checked using the Cochran *C*-test. The Student-Newman-Keuls (SNK) test was used for a posteriori multiple comparison of means (Underwood, 1997).

RESULTS

An encrusting calcareous layer completely covered the substrate in all samples and it was mostly constituted by the Corallinales *Mesophyllum alternans* (Foslie) Cabioch and Mendoza; *Mesophyllum macroblastum*

TABLE 2. – Results of SIMPER test							
[°] axa	Average abundance	Average abundance	Contribution %				
sland	-30 m	-40 m					
Flabellia petiolata Peyssonnelia rubra Halimeda tuna Vomersleyella setacea Peyssonnelia squamaria Meredithia microphylla Osmundea pelagosae Canardina typus Eupogodon planus Valonia macrophysa Acrodiscus vidovichii Dictyota linearis	$\begin{array}{c} 34.9\\ 20.2\\ 27.7\\ 22.5\\ 3.6\\ 0.5\\ 4.2\\ 1.4\\ 0.3\\ 1.6\\ 0.5\\ 1.5\end{array}$	$\begin{array}{c} 4.4 \\ 47.9 \\ 1.1 \\ 6.2 \\ 10.0 \\ 8.7 \\ 7.4 \\ 4.4 \\ 2.5 \\ 0.8 \\ 1.6 \\ 0.0 \end{array}$	$18.6 \\ 17.2 \\ 16.6 \\ 11.7 \\ 5.8 \\ 4.9 \\ 4.3 \\ 3.4 \\ 1.4 \\ 1.2 \\ 1.0 \\ 0.9$				
30m	coast	island					
Flabellia petiolata Halimeda tuna Veyssonnelia rubra Vomersleyella setacea Zanardina typus Fricleocarpa fragilis Osmundea pelagosae Peyssonnelia squamaria Acrodiscus vidovichii Valonia macrophysa Dictyota linearis Meredithia microphylla	$5.1 \\ 1.9 \\ 34.6 \\ 7.9 \\ 10.0 \\ 5.2 \\ 3.5 \\ 1.1 \\ 1.6 \\ 0.1 \\ 0.7 \\ 1.3 $	$\begin{array}{c} 34.9\\ 27.7\\ 20.2\\ 22.5\\ 1.4\\ 0.0\\ 4.2\\ 3.6\\ 0.5\\ 1.6\\ 1.5\\ 0.5\end{array}$	$20.8 \\ 18.6 \\ 13.2 \\ 12.6 \\ 7.0 \\ 3.7 \\ 2.9 \\ 2.7 \\ 2.03 \\ 1.1 \\ 0.9 \\ 0.9 \\ 0.9$				

(Foslie) W.H. Adey and *Lithophyllum pustulatum* (J.V. Lamouroux) Foslie were also present with lower abundance. A total of 91 macroalgal species were identified as epiphytes of encrusting Corallinales, among them 11 Ochrophyta, 8 Chlorophyta and 72 Rhodophyta (Appendix 1).

PERMANOVA analysis detected a significant interaction between Condition and Depth; the pairwise



FIG. 3. – Non-metric multidimensional scaling ordination based on Bray-Curtis similarity. White, small islands; black, continental coasts; triangles, -30 m; circles, -40 m.

tests showed that the structure of assemblages of the two studied depths differed off islands but not along continental coasts and differences between conditions were significant only at 30 m depth (Table 1). The nMDS showed shallow assemblages off islands and continental coasts to be clearly segregated, while deep assemblages of both types of shore were close to each other. Moreover, deep and shallow assemblages were more separated off islands than off continental coasts (Fig. 3).

Off islands, the main species characterizing shallow coralligenous assemblages were represented by the Chlorophyta *Flabellia petiolata*, *Halimeda tuna* and *Valonia macrophysa*, the Rhodophyta *Womersleyella setacea* and the Ochrophyta *Dictyota linearis*, while *Meredithia microphylla*, *Osmundea pelagosae*, *Zanardina typus*, *Eupogodon planus* and *Peyssonnelia* spp. were abundant in deeper assemblages (Table 2).



FIG. 4. – Species number per sample and total percentage cover of marcoalgal coralligenous assemblages (encrusting Corallinales excluded). C, continental coast; I, small islands; numbers indicate sampling depths.

At 30 m depth, off the continental coasts the percent cover of erect Udoteaceae (*Flabellia petiolata* and *Halimeda tuna*), *Womersleyella setacea*, *Osmundea pelagosae*, *Valonia macrophysa* and *Dictyota linearis* was lower than off the islands, while *Peyssonnelia rubra*, *Zanardina typus*, *Tricleocarpa fragilis*, *Acrodiscus vidovichii* and *Meredithia microphylla* were more abundant.

ANOVA detected significant interactions between Condition and Depth for both total percentage cover and species number (Table 3). The total percentage cover was lower off continental coasts than off islands at both depths, while the species number showed the same pattern in the deeper assemblages but with an opposite pattern for the shallower one. For both analyses, differences between depths were significant only for islands (Fig. 4).

Source	df	Species number MS	F	Р	Percentage cover MS	F	Р
Condition (C) Depth (D) C×D Site (C×D) Residual Total	1 12 1 32 47	1.687 7.520 48.715 136.687 10.87	0.03 0.15 4.48 2.81	0.855 0.701 0.001 0.119	16248.4012 1984.9071 1068.2102 576.3864 165.8652	15.21 1.86 6.44 0.54	0.002 0.197 0.000 0.476
C=0.323 (ns) SNK test C×D -30 m C -40 m C Coast -3 Island -3		Coast Coast -30 m -30 m	> Island < Island = -40 m < -40 m	C=0.158 (ns) -30 m -40 m Coast Island	Coast Coast -30 m -30 m	< Island < Island =-40 m >-40 m	

TABLE 3. - Results of ANOVA analyses on species number and total percentage cover. Significant results are in bold.

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DISCUSSION

The present study shows that macroalgal coralligenous assemblages differ between depths but this pattern is not consistent along the continental coasts. Consequently, differences between assemblages related to different environmental conditions were more evident in the shallower zone of distribution of coralligenous habitats.

Off the islands, the differences between assemblages colonizing the two studied depths were mostly related to a higher percentage cover of erect Udoteaceae (Flabellia petiolata and Halimeda tuna) in the shallower assemblages and a higher percentage cover of sciaphilous species in the deeper assemblages. A high abundance of Udoteaceae in the shallower zone of coralligenous habitats has been already described in other Mediterranean areas (Ballesteros, 1992; 2006) and it may be considered characteristic of this bathymetric range. On the other hand, the species characterizing the deeper assemblages (Meredithia mycrophylla, Zanardina typus, Eupogodon planus and Peyssonnelia spp.) are typical of coralligenous habitats (Piazzi et al., 2010). Off the continental coasts, the lack of significant differences between the two depths examined were mostly related to the fact that assemblages of both depths were characterized by low cover of erect Udoteaceae and other moderate sciaphilous species, such as Valonia macrophysa and Dictyota linearis, besides a high abundance of typical coralligenous species. This pattern could be related to a reduction of light penetration due to an increase in sedimentation and in other human-induced pollutants (Petrilli et al., 1979; Airoldi et al., 1996; Balata et al., 2005). In fact, previous experimental investigations showed that erect Udoteaceae were sensitive to disturbances such as sedimentation and colonization of the invasive species Caulerpa racemosa (Forsskål) C. Agardh var. cylindracea (Sonder) Verlaque, Huisman et Boudouresque (Balata et al., 2007a, 2007b; Piazzi and Balata, 2008).

In the shallower assemblages the total percentage cover was lower along continental coasts than around islands due to the decrease in erect Udoteaceae; an opposite pattern was observed for the species number per plot. Around islands, richness increased in deeper assemblages following a common pattern for rocky subtidal systems (Garrabou *et al.*, 2002). Along the continental coasts, the lack of Udoteaceae probably favoured the spread of less competitive species, leading to an increase in richness in shallower assemblages and altering patterns of vertical distribution.

Species richness is similar along the coasts and islands (80 vs 83 species), but the decrease of differences among assemblages related to different depths along the coasts may lead to a higher spatial homogenization and an impoverishment of the system (Olden *et al.*, 2004). In fact, beta diversity, defined as the change of species composition and abundance along environmental gradients (between-habitat diversity), is an important aspect for ecological studies and contributes highly to the total diversity of marine systems (Legendre *et al.*, 2005; Gray, 1997, 2000). It is known that changes in alphadiversity can be completely uncoupled from betweenhabitat homogenization (Olden and Poff, 2003); thus, the replacement of locally distinctive assemblages with widespread species caused by disturbance could lead to a decrease in beta-diversity while alpha-diversity could remain unchanged (Smart *at al.*, 2006).

This correlative study does not reveal any causeeffect relationships; however, patterns detected in the present study are in agreement with the results of manipulative studies (Balata *et al.*, 2007a, 2007b), suggesting that different environmental conditions, mostly related to different levels of sedimentation and pollution, can be the cause of the observed patterns. Further studies considering different kinds of disturbance are necessary in order to test the model that environmental conditions can modify vertical patterns of distribution of coralligenous assemblages. Moreover, sessile animals, which in the present study were not considered, are determinant for the structure and functioning of these systems (Cocito *et al.*, 2002; Cocito, 2004) and they may be an interesting topic for further research.

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Appendix 1. – Floristic list

	Coast		Isla	Island	
TAXA	-30 m	-40 m	-30 m	-40 m	
FUCOPHYCEAE					
Asperococcus bullosus J.V. Lamouroux	+	+	+	+	
Cladosiphon irregularis (Sauvageau) Kylin	-	-	+	-	
Cutleria chilosa (Falkenberg) P.C. Silva (sporophyte "Aglaozonia")	-	-	+	-	
Dictyota linearis (C. Agardh) Greville	+	-	+	-	
Halopteris filicina (Grateloup) Kutzing Nereja filiformis (L. Agardh) Zanardini	+	+	+	+	
Spermatochnus paradoxus (P.H. Roth) Kützing	т -	-	-	+	
Sphacelaria cirrosa (P.H. Roth) C. Agardh	+	+	+	+	
Śphacelaria plumula Zanardini	+	+	+	+	
Stictyosiphon adriaticus Kützing	-	-	-	+	
Zanardinia typus (Nardo) P.C. Silva	+	+	+	+	
Chlorophyta					
Cladophora echinus (Biasoletto) Kützing	+	+	+	+	
Cladophora prolifera (Roth) Kützing	+	+	+	+	
Flabellia petiolata (Turra) Nizamuddin	+	+	+	+	
Halimeda tuna (J. Ellis et Solander) J.V. Lamouroux	+	-	+	+	
Microalciyon lenuius Decaisile ex J.E. Gray Palmonbullum crassum (Naccari) Rabanbarst	-	-	+	+	
Pseudochlorodesmis furcellata (Zanardini) Børgesen	+	+	+	+	
Valonia macrophysa Kützing	+	+	+	+	
KHODOPHYTA Agrodisaus vidoviskii (Managhini) Zanardini					
Acrosorium ciliolatum (Harvey) Kylin	+	+	+	-	
Acrothamnion preissii (Sonder) Wollaston	+	+	+	+	
Aglaothamnion tenuissimum (Bonnemaison) Feldmann-Mazoyer	+	+	+	+	
Aglaothamnion tripinnatum (C. Agardh) Feldmann-Mazoyer	+	-	-	-	
Amphiroa rubra (Philippi) Woelkerling	+	-	+	-	
Antithamnion cruciatum (C. Agardh) Nageli	+	+	+	+	
Antinamnion nelefociaaum Fulik Anthithamnion nilifarum Cormaci at G. Eurnari	+	+	-	-	
Antithamnion tenuissimum (Hauck) Schiffner	+	-+	+	+	
Apoglossum gregarium (Dawson) M.J. Winne	+	+	+	+	
Apoglossum ruscifolium (Turner) J. Agardh	+	+	+	+	
Botryocladia botryoides (Wulfen) Feldmann	+	+	+	+	
Brongniartella byssoides (Goodenough et Woodward) F. Schmitz	-	-	-	+	
Ceramium bisnorum Ballantine	+	-	+	+	
Ceramium cimbricum H.E. Petersen	-	-	+	+	
Ceramium codii (H. Richards) Feldmann-Mazoyer	+	+	+	+	
Ceramium diaphanum (Lightfoot) P.H. Roth	+	-	+	-	
Ceramium flaccidum (Kützing) Ardissone	+	+	+	+	
Ceramium tenerrimum (G. Martens) Okamura	-	-	+	-	
Champia parvula (C. Agardii) Harvey Chandria capillaris (Hudson) M I. Wynne	+	+	+	+	
Chrysymenia ventricosa (IV Lamouroux) I. Agardh	_	+	-	-	
Contarinia peyssonneliaeformis Zanardini	+	-	-	-	
Contarinia squamariae (Meneghini) Denizot	+	+	+	+	
Dasya corymbifera J. Agardh	-	-	-	+	
Dasya ocellata (Grateloup) Harvey	+	+	+	+	
Dasya rigiaula (Kutzing) Ardissone	+	-	+	+	
<i>Eurogodon planus</i> (C. Agardh) Kützing	+	+	-+	+	
<i>"Falkenbergia rufolanosa</i> (Harvey) F. Schmitz <i>«stadium</i> sporophyte of	•	·		•	
Asparagopsis armata Harvey	+	-	+	+	
Feldmannophycus rayssiae (Feldmann et Feldmann-Mazoyer) Augier et Boudouresque	+	+	+	+	
Gelidium bipectinatum G. Furnari	+	+	+	+	
Griffithsia schousboei Montagne Habdyction mirabile Zapardini	+	+	+	-	
Hernosinhonia secunda (C. Agardh) Ambronn	- -	-	+	-	
Heterosiphonia crispella (C. Agardh) M.J. Wynne	+	+	+	+	
Hypoglossum hypoglossoides (Stackhouse) Collins et Harvey	+	+	+	+	
Irvinea boergesenii (Feldmann) R.J. Wilkes, L.M. McIvor et Guiry	-	+	-	-	
Jania adhaerens J.V. Lamouroux	+	-	+	-	
Laurencia chondrioides Børgesen	+	+	+	+	
Lomentaria ercegovicii Verlague Boudouresque Meinesz Circud et Marcot Cognougniot	+	+	+	-	
Meredithia microphylla (J. Agardh) J. Agardh	+	-+	+ +	-+	
Monosporus pedicellatus (J.E. Smith) Solier	+	+	+	+	

Appendix	1	(cont.)	- Floristic	list
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	Co	ast	Island	
TAXA	-30 m	-40 m	-30 m	-40 m
Neurocaulon foliosum (Meneghini) Zanardini	+	+	-	+
Osmundea pelagosae (Schiffner) F.W. Nam	+	+	+	+
Peyssonnelia rubra (Greville) J. Agardh	+	+	+	+
Peyssonnelia squamaria (S.G. Gmelin) Decaisne	+	-	+	+
Peyssonnelia stoechas Boudouresque et Denizot	+	+	-	-
Phyllophora crispa (Hudson) P.S. Dixon	-	+	-	+
Plocamium cartilagineum (Linnaeus) P.S. Dixon	+	+	+	+
Polysiphonia elongata (Hudson) Sprengel	+	-	+	+
Polysiphonia furcellata (C. Agardh) Harvey	+	+	+	+
Polysiphonia perforans Cormaci, G. Furnari, Pizzuto et Serio	+	+	+	+
Polysiphonia subulifera (C. Agardh) Harvey	+	+	+	+
Pterothamnion plumula (J. Ellis) Nägeli	+	+	-	-
Ptilothamnion pluma (Dillwyn) Thuret	+	+	+	+
Radicilingua reptans (Kylin) Papenfuss	+	-	+	+
Rhodophyllis divaricata (Stackhouse) Papenfuss	+	+	+	+
Rhodymenia ardissonei J. Feldmann	+	+	+	+
Rodriguezella pinnata Ercegovic	+	+	+	+
Rodriguezella strafforelloi F. Schmitz	+	+	-	+
Rytiphlaea tinctoria (Clemente) C. Agardh	+	+	-	+
Schmitzia neapolitana (Berthold) P.C. Silva	+	+	+	+
Spermothamnion repens (Dillwyn) Rosenvinge	+	-	-	+
Sphaerococcus coronopifolius Stackhouse	+	+	-	-
<i>Spyridia filamentosa</i> (Wulfen) Harvey	-	-	-	+
Tricleocarpa fragilis (Linnaeus) Huisman et R.A. Towsend	+	+	-	-
Womersleyella setacea (Hollenberg) R.E. Norris	+	+	+	+
Wrangelia penicillata (C. Agardh) C. Agardh	+	-	+	-