Daniele Curiel, Chiara Miotti, Emiliano Checchin,
Andrea Rismondo, Sara Kaleb, Annalisa Falace

PATTERNS OF DIVERSITY OF MACROALGAL ASSEMBLAGES ON BIOGENIC OUTCROPS IN THE NORTHERN ADRIATIC SEA

Riassunto. *Modelli di distribuzione delle macroalghe degli affioramenti rocciosi del Nord Adriatico.*
La diversità delle macroalghe sugli affioramenti biogenici dell'Alto Adriatico è stata analizzata a diverse scale spaziali: plot (replica), sito (affioramento), area (affioramenti distanti 1-2 km), località (Venezia vs. Trieste), regione (intero bacino). Le macroalghe (173 specie) mostrano un'elevata variabilità nel numero di taxa e copertura a scala di affioramento. La β-diversità aumenta con l'area considerata fino a scala di località. La componente macroalgale mostra significative differenze tra affioramenti posti sottocosta e al largo, mentre l'incidenza dell'elevazione dal substrato degli affioramenti è significativa solo sottocosta. Nelle aree prossime alla costa gli affioramenti bassi (Type 1) sono caratterizzati da taxa ubiquitari, mentre le specie incrostanti (es. *Peyssonnelia* spp. e *Lithophyllum pustulatum*) presentano maggior copertura sugli affioramenti più elevati (Type 2). Al largo invece entrambi i tipi di affioramenti si caratterizzano per elevate coperture di alghe incrostanti dei generi *Lithophyllum* e *Peyssonnelia*.

Summary. The patterns of diversity of macroalgal assemblages on calcareous bio-concretions in the northern Adriatic Sea have been analyzed at different spatial scales: plot (each replicate), site (outcrop), area (groups of outcrops distant 1-2 km), location (Venice vs. Trieste) and region (the whole study area). The macroalgae (173 taxa) displayed a high variability in the number of taxa and coverage at outcrop scale. The β-diversity scaled up until location level. The macroalgal assemblages showed significant differences between the inshore and the offshore areas, while differences between high and low outcrops resulted significant only in the inshore sites. In coastal areas lower outcrops (Type 1) were characterized by ubiquitous taxa while the encrusting algae (i.e. *Peyssonnelia* spp. and *Lithophyllum pustulatum*) were more abundant on higher outcrops (Type 2). Offshore, both types showed a higher coverage of encrusting coralline algae of the genera *Lithophyllum* and *Peyssonnelia*.

Keywords: macroalgae, biogenic outcrops, coralligenous, species diversity, Adriatic Sea.

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INTRODUCTION

The Coralligenous represents one of the most important Mediterranean benthic ecosystems because of its extent, biodiversity and implications for fisheries and carbon regulation (BALLESTEROS, 2006; UNEP-MAP-RAC/SPA, 2008; MARTIN et al., 2014). These complex biogenic structures result from the dynamic equilibrium between the building activities of calcareous encrusting algae and sessile animals (mostly Cnidaria, Polychaeta and Bryozoa) and the physical and biological erosional processes (BALLESTEROS, 2006). Two main coralligenous morphologies have been recognized: i) banks are flat structures (ranging from 0.5 to 4 m in height) formed over more or less horizontal substrates; ii) rims develop on vertical cliffs and are generally shallower than banks (PÉRÈS & PICARD, 1964; LABOREL, 1987; BALLESTEROS, 2006).

The northern Adriatic Sea is scattered with some hundreds biogenic outcrops (BRAGA & STEFANON, 1969; NEWTON & STEFANON, 1975) characterized by benthic assemblages similar to those reported for the coralligenous (CASELLATO & STEFANON, 2008), even if with striking differences that make them unique (CURIEL et al., 2012). Information on these outcrops dates back to the end of the XVIIIth century (OLIVI, 1792) and their topography

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and geology are well known (BRAGA & STEFANON, 1969; NEWTON & STEFANON, 1975). In the last 10-15 years several studies on macroalgae (CURIEL et al., 2001, 2010, 2012, 2014; CURIEL & MOLIN, 2010; KALEB et al., 2011; GORDINI et al., 2012) and zoobenthos (MIZZAN, 1992; GABRIELE et al., 1999; CASELLATO et al., 2005, 2007; CASELLATO & STEFANON, 2008; PONTI & MESCALCHIN, 2008; MOLIN et al., 2010, PONTI et al., 2011; MIOTTI et al., 2014; FALACE et al., 2015) have been conducted.

The aim of this paper is to highlight the pattern of macroalgal diversity of these structures at different spatial scales (from few meters to several kilometers) comparing outcrops with different extent and locations.

MATERIALS AND METHODS

The data analyzed come from previous studies (fig. 1). For sampling methods, qualitative and coverage data, see CURIEL et al. (2012). Species richness was partitioned at different spatial scale: plot (each replicate), sites (outcrop α-sites), areas (outcrops within 1-2 km β-areas), location (off Chioggia-Venezia and off Grado-Trieste β-location) and region (the whole study area β-region) using the additive approach proposed by CRIST et al. (2003). This analysis was also applied to morphological groups (turfs, erect, encrusting). The outcrops were separated into inshore (< 4 km from the cost) and offshore ones (> 4 km from the cost). The arbitrary limit of 4 km was chosen based on abiotic data available from the Veneto region (Secchi disc, total P and total N concentration) (ARPAV, 2009: fig. 2). The chemical and physical data (obtained from ARPAV publications - 2009) were averaged considering spring and autumn, and the area between the rivers Brenta and Tagliamento. The inshore data refer to a station located 500 m off the coast and offshore data refer to

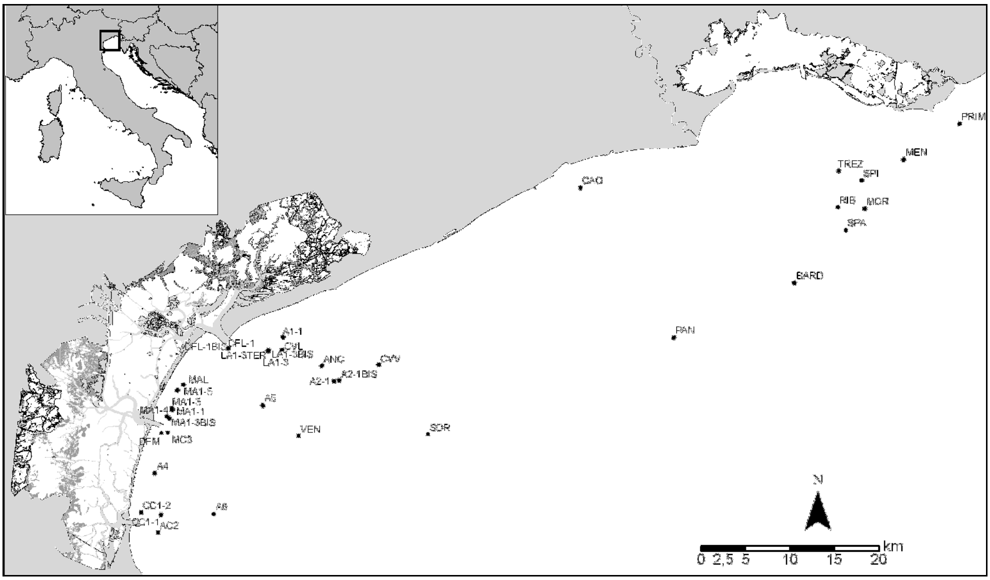

Fig. 1. Location of the investigated outcrops.

distant station, located approximately 4 km off the coast. In relation to the methods, the concentrations of total P and total N were determined in samples of filtered water by ARPAV laboratory (ARPAV, 2009).

This boundary is also in accordance with the mathematical model of outflows from the lagoon of Venice (D'ALPAOS & MARTINI, 2005). Also the extent of the outcrops (Type 1- low outcrops 0.5-1m height; Type 2- high outcrops up to 2-4 m height) was considered (table 1).

Multivariate statistical analyses (ANOSIM, PERMANOVA and SIMPER) were carried out on macroalgal coverage. After a preliminary ANOSIM analysis, that showed a high similarity between the plots belonging to the same outcrop (Global R > 0,9 and

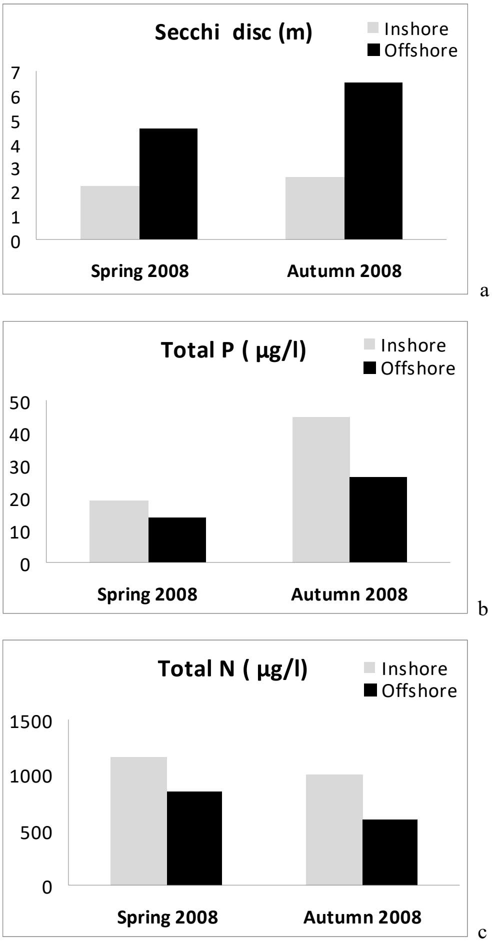

Fig. 2. Values of trasparency (Secchi disc) (a), concentration of total P (b) and total N (c) in spring and autumn 2008 (ARPAV, 2009).

significance statistic level 0,01%), they were considered as replicates and the data averaged. The PERMANOVA (Anderson, 2001) was performed considering two crossed factors: Type (Type 1 vs. Type 2) and Condition (Inshore vs. Offshore). Bray-Curtis measures of similarities in log (x+1) transformed data were used to calculate a matrix of distances between pairs of samples. The SIMPER tests (Clarke & Warwick, 2001) analyzed the comparisons between the levels of the Condition × Type and interaction that were significant in the pairwise tests (PERMANOVA).

Species richness and total coverage were analyzed by non-parametric Mann-Whitney test utilizing the same factors of PERMANOVA analysis (Type, Condition). Also coverages, distinguishing sciaphilous, photophilous, encrusting, turf and erect layer, were tested with the Mann-Whitney test.

Table 1. Outcrops morphology (Type 1= low outcrops; Type 2= high outcrops), depth and distance from the coast.

Site	**Morphology (Type)**	**Depth (m)**	**Coast dist. (km)**	**Site**	**Morphology (Type)**	**Depth (m)**	**Coast dist. (km)**
A1-1	Type 2	14	3	LA1-3TER	Type 2	14	3,9
A2-1	Type 1	19	9,7	MA1-1	Type 1	10	1
A2-1BIS	Type 1	19	9,8	MA1-3	Type 1	10	1,9
A4	Type 1	10	1,9	MA1-3BIS	Type 1	10	1,9
A5	Type 1	17	8,5	MA1-4	Type 1	8	1
A6	Type 1	20	8,3	MA1-5	Type 1	7	1,4
AC2	Type 1	15	2,2	MAL	Type 1	9	1,7
ANC	Type 2	18	7,5	MC3	Type 1	12	1
BARD	Type 2	19	19	MEN	Type 1	14	4,8
CAO	Type 1	10	2,8	MOR	Type 2	19	10,9
CC1-1	Type 1	16	1,2	PAN	Type 2	25	21,2
CC1-2	Type 1	9	2,5	PRIM	Type 2	10	2,5
CVL	Type 2	20	9,9	RIB	Type 1	21	11,5
CVV	Type 2	15	4,3	SPI	Type 2	15	7,4
DFL-1	Type 1	10	0,5	SOR	Type 2	22	19,3
DFL-	Type 1	10	0,5	SPA	Type 2	19	13,8
DFM	Type 1	9	0,7	TREZ	Type 1	13	7,6
LA1-3	Type 2	14	3,9	VEN	Type 1	20	13,3
LA1-	Type 2	14	3,9				

Results

A total of 173 macroalgal taxa, of which 124 Rhodophyta, 25 Ochrophyta and 24 Chlorophyta were found. The mean number of taxa for outcrop was 25.6 and the mean coverage 14.8%. At all the considered spatial scales (from plot to region) the number of species was higher on the offshore outcrops than on the inshore ones (fig. 3). Only 6 taxa showed a frequency > 50%, while 60 taxa were collected with a frequency < 5%. Turf algae represented ca. 60% of total taxa. Rhodophyta ranged from 50 to 100% of the total number of taxa on each outcrop, Chlorophyta from 0 to 33% and Ochrophyta from 0 to 19%.

Among the most common species (frequency > 40%) were the Rhodophyta *Rhodymenia ardissonei, Radicilingua thysanorhizans, Rhodophyllis divaricata*, *Lithophyllum pustulatum, Cryptonemia lomation*, *Gracilariopsis longissima* and the Chlorophyta *Ulva laetevirens* and *Pseudochlorodesmis furcellata.* The Ochrophyta were rare and the most frequent (20-30%) were *Sphacelaria plumula*, *Dictyota* spp. and *Halopteris filicina*.

As for the frequency, also the coverage showed a high variability among outcrops. The Rhodophyta showed a mean coverage of 10.6% ±20.2, the Ochrophyta of 1.9% ±8.0 and the Chlorophyta of 1.9% ±3.8. The more abundant taxa were the Rhodophyta *Peyssonnelia* spp., *Lithothamnion philippii, L. pustulatum, R. ardissonei* and *C. lomation.* For the Ochrophyta *Zanardinia typus* showed the higher coverage and for the Chlorophya *U. laetevirens.*

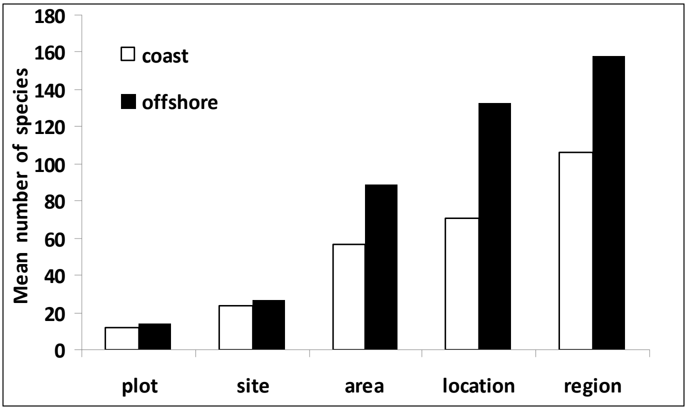

Fig. 3. Mean number of species at different sampling scales on inshore and offshore outcrops.

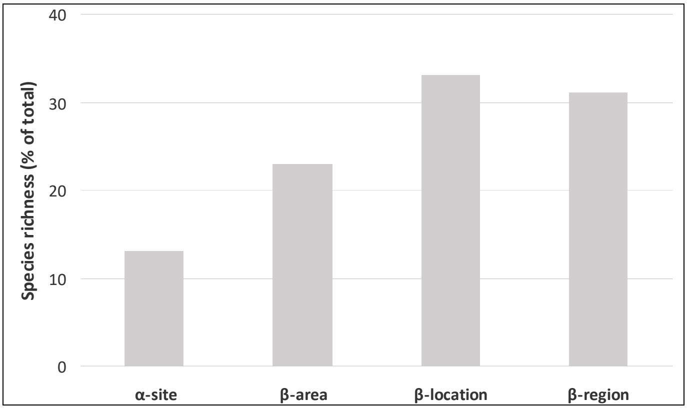

Fig. 4. Additive partition of species richness across different spatial scales.

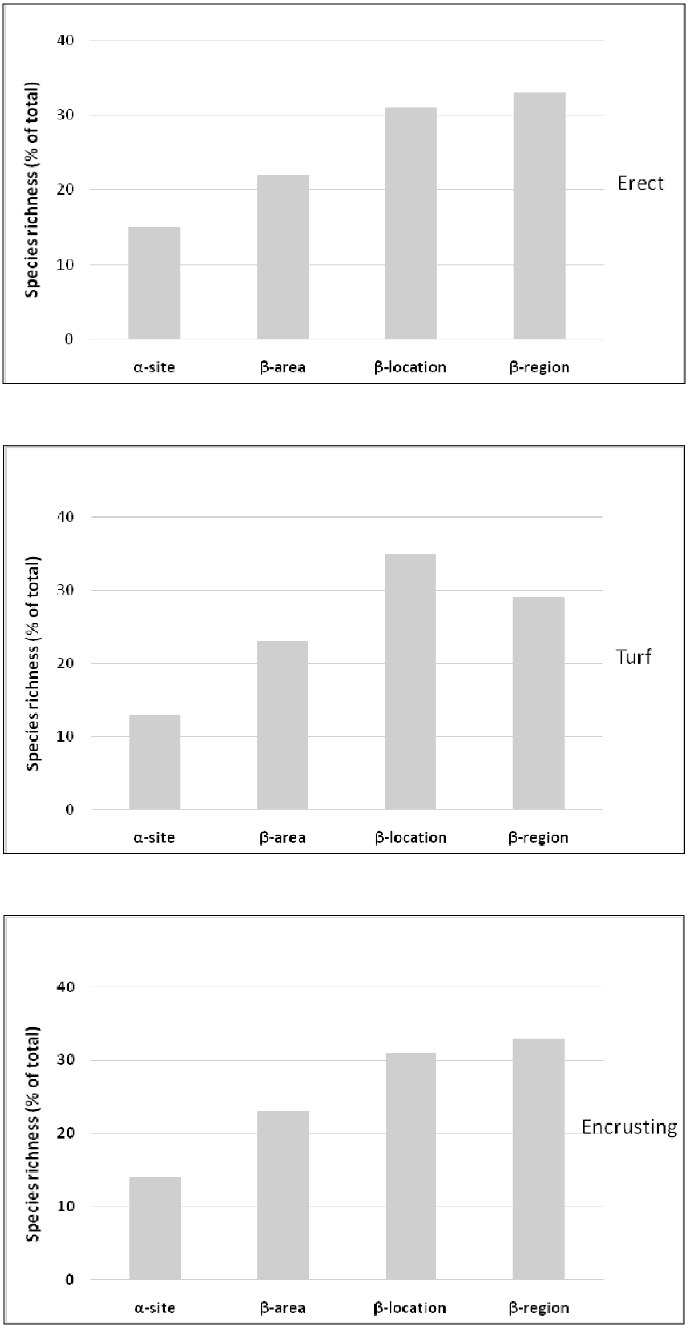

Fig. 5. Additive partition of morphological groups richness across the sampling spatial scales.

The contribution to the total richness increased from site to location level, which alone explained about 33%, while the variation of species richness at the regional scale was lower (fig. 4).

When considering the morphological groups, a similar trend was observed also for the turfs algae, while the encrusting and erect algae showed a continuous increasing from site to regional scale (fig. 5).

The PERMANOVA test (table 2) showed significant differences among the Type (Type 1 vs. Type 2) and Condition (inshore vs. offshore) and a significant interaction between the two factors (Co x Ty). The pairwise tests showed that the algal assemblages of the Types 1 and Types 2 differed on the inshore sites and that the differences between Conditions were significant for both the Types. Inshore, the Type 1 outcrops were distinguished by more tolerant ubiquitous taxa as the green algae *U. laetevirens* and *Chaetomorpha linum*, laminar red algae as *R. ardissonei*, *C. lomation*, *R. thysanorhizans*, *Nitophyllum punctatum*; while the Type 2 outcrops were characterized by laminar red algae and the encrusting *Peyssonnelia* sp. and *L. pustulatum* (table 3).

Offshore, both Types showed a higher coverage of encrusting coralline algae (i.e. *L. pustulatum, Lithophyllum incrustans, Lithophyllum stictaeforme, L. philippii*), and *Peyssonnelia* (*P. rosa-marina, P. harveyana, P. dubyi, P. squamaria, P. polymorpha*) (table 3).

The Mann-Whitney test showed no significant differences (P>0,05) in species richness and total coverage between inshore vs. offshore outcrops and between Type 1 vs. Type 2 (fig. 6). Nevertheless, significant differences in the coverage between inshore vs. offshore outcrops were detected for sciaphilous taxa, and for the encrusting and erect morphologies. Between Type 1 vs. Type 2 outcrops a significant difference in the coverage was observed only for the encrusting algae (fig. 7).

Table 2. Results of PERMANOVA analysis; significant results are in bold.

Source	df	MS	Pseudo-F	P(perm)
Condition (Co)	1	17494	6,553	**0,001**
Type (Ty)	1	7298,8	2,7339	**0,002**
CoxTy	1	7351,5	2,7537	**0,004**
Residual	33	2669,7		
Total	36			
Pairwise test (CoxTy)		inshore	type 1, type 2	**0,002**
		offshore	type 1, type 2	1,89
		Type 1	coast, offshore	**0,001**
		Type 2	coast, offshore	**0,001**

DISCUSSION

The macroalgal assemblages of the studied outcrops are characterized by high variability both in richness (from 6 to 97 taxa per outcrops) and coverage (from 0 to 147%).

Indications that the benthic assemblages of the northern Adriatic outcrops differ according to distance from the coast and depth, were previously provided by PONTI et al. (2011), CURIEL et al. (2012) and FALACE et al. (2015). In accordance with PONTI et al.

Table 3. Results of SIMPER test.

Taxa	Average abundance	Average abundance	Contribution %
Inshore	**Hight stone**	**Low stone**	
Ulva laetevirens	0,53	259,17	31,76
Rhodymenia ardissonei	22,01	98,1	15,15
Cryptonemia lomation	17,31	93,61	12,42
Rhodophyllis divaricata	43,16	26,49	8,21
Radicilingua thysanorhizans	0,84	57,38	5,96
Chaetomorpha linum	0	29,45	3,22
Dictyota dichotoma var. *intricata*	0	26,77	1,92
Nitophyllum punctatum	0	23,6	1,74
Aglaothamnion sp.	1,27	7,65	1,55
Peyssonnelia sp.	8,83	0,42	1,42
Gracilariopsis longissima	0,59	7,56	1,41
Dasya hutchinsiae	0,02	7,72	1,35
Peyssonnelia squamaria	0	6,13	1,29
Lithophyllum pustulatum	8,05	1,82	1,19
Ceramium cimbricum	8,8	0	1,05
Rhodymenia pseudopalmata	1,33	3,6	0,85
Low stone (Type 1)	**Offshore**	**Inshore**	
Ulva laetevirens	53,5	259,17	20,69
Lithophyllum pustulatum	365,25	1,82	13,84
Peyssonnelia rosa-marina	86,81	0,34	8,97
Rhodymenia ardissonei	16,52	98,1	8,86
Cryptonemia lomation	0,75	93,61	7,13
Peyssonnelia harveyana	311,6	0	6,66
Radicilingua thysanorhizans	19,85	57,38	4,23
Aglaothamnion sp.	73,03	7,65	4,22
Peyssonnelia dubyi	146	0	4,07
Rhodophyllis divaricata	0,25	26,49	2,48
Chaetomorpha linum	0,27	29,45	2,08
Gelidium pusillum	55,9	0,14	2,01
Cutleria chilosa	23,41	0,11	1,52
Dictyota dichotoma var. *intricata*	0	26,77	1,3
Nitophyllum punctatum	0	23,6	1,17
Lithothamnion philippii	5,63	0,14	0,96
High stone (Type 2)	**Offshore**	**Inshore**	
Lithophyllum pustulatum	453,8	8,05	14,8
Lithothamnion philippii	237,7	0	12,73
Peyssonnelia rosa-marina	153,36	0,4	9,49
Peyssonnelia harveyana	66,02	0	6,45
Rhodymenia ardissonei	107,49	22,01	4,71
Rhodophyllis divaricata	1,83	43,16	4,42
Lithophyllum incrustans	143,78	0	4,12
Cryptonemia lomation	70,88	17,31	3,98
Peyssonnelia dubyi	93,71	0	3,54
Lithothamnion sp.	81,22	0	3,42
Gelidium pusillum	62,16	0	3,38
Peyssonnelia squamaria	300,97	0	3,03
Peyssonnelia polymorpha	335,1	0	2,92
Lithophyllum stictaeforme	23,7	0	2,78
Zanardinia typus	264,55	0	2,21
Peyssonnelia sp.	3,09	0	1,56
Pseudochlorodesmis furcellata	176,52	0,05	1,35
Halymenia floresii	158,74	0	1,26
Cutleria multifida	123,46	0	1,02
Derbesia marina	20,62	0	0,95
Ceramium cimbricum	1,39	8,8	0,93

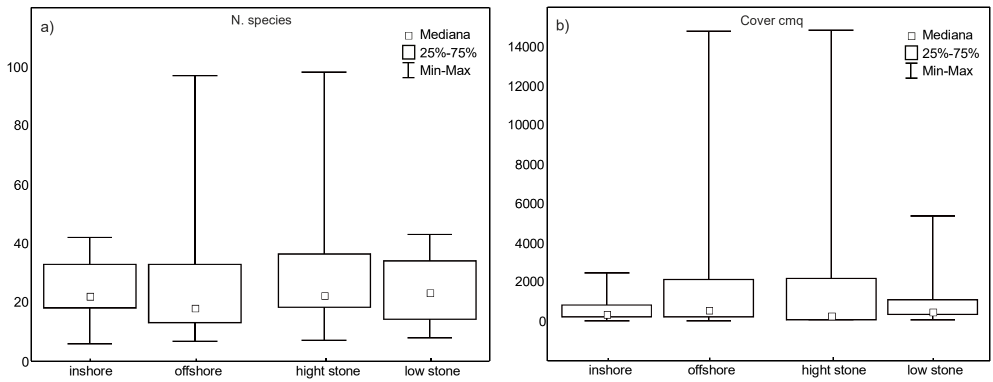

Fig. 6. Species number a) and total coverage boxplot b) for the factor distance (inshore-offshore) and morphology type (low - high rocky outcrops).

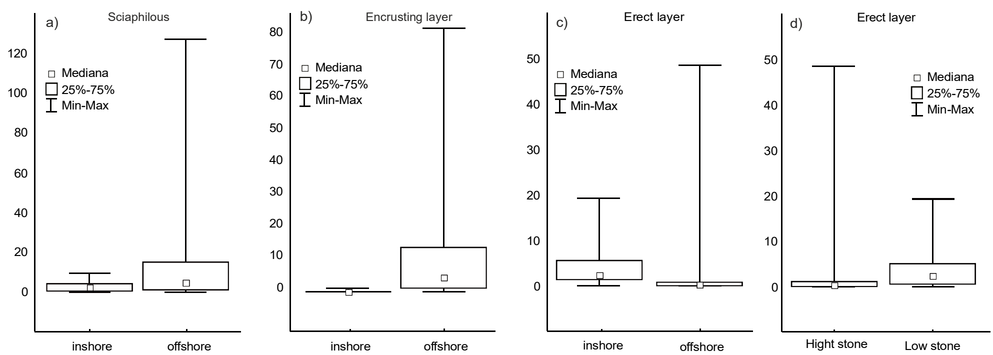

Fig. 7. Significant differences in coverage for ecological groups of both factors: coastal distance (a, b and c) and morphology type (d).

(2015), the greatest diversity comes from areas that are distant hundreds of kilometres, and not at site scale. An opposite pattern was detected by PIAZZI et al. (2010) and BALATA & PIAZZI (2008), who observed high values of diversity at small spatial scales (plot, sample). These differences can be ascribed to both a greater 3-dimensional complexity of the bioconcretion, due to the presence of large anthozoans, bryozoans and alcyonarians and a lower physical disturbance that characterize the western Mediterranean coralligenous since historical times (PIAZZI et al., 2004; BALLESTEROS, 2006). Although we cannot provide specific measurements of field to support this hypothesis, it is in agreement with our personal observation during diving activities.

Regarding the physical disturbance of the northern Adriatic Sea, studies on long term series show gradual increase of eutrophication pressure in the least 30 years, occurred during the 1970s until the mid 1980s, followed by a reversal of the trend, particularly marked in the 2000s. The improvement was marked by a clear reduction in the concentration of phosphate and ammonia in the coastal area, probably due to the adoption of new regulations for the control of nutrient loads while no decrease in nitrate concentrations was observed (SOLIDORO et al., 2009). The long term series also show a global tendency towards chlorophyll a reduction; in addition, very little evidence supports the hypothesis of significant warming of northern Adriatic waters during the last 30 years (MOZETIČ et al., 2010).

The total macroalgal richness β-diversity pattern was driven by the pattern of turf algae that represented ca. the 60% of total taxa. Even though with low coverage, several species characteristic of the Mediterranean coralligenous were found (*L. stictaeforme, Lithothamnion minervae, L. philippii, Mesophyllum alternans, Mesophyllum macroblastum, Neogoniolithon mamillosum*).

One of the most important factors driving assemblage heterogeneity is spatial variability of environmental parameters (VEECH & CRIST, 2007; MATIAS et al., 2011; HEWITT et al., 2005), thus the low mean coverage of the encrusting layer, if compared to Mediterranean coralligenous (BALLESTEROS, 2006; PIAZZI et al., 2004), could be due to the high variability of the environmental parameters of the northern Adriatic Sea. The coast is characterized by low salinity and high concentration of inorganic nutrients, organic matter, and chlorophyll a while higher salinity and lower concentrations of inorganic nutrients and chlorophyll a distinguish the offshore stations (BERNARDI-AUBRY et al., 2006; FALACE et al., 2015). The macroalgal assemblages showed significant differences between the inshore and the offshore areas, while the interaction with the morphology type occurred only for the inshore outcrops. In coastal areas lower outcrops (Type 1) were characterized by ubiquitous taxa while the encrusting algae (i.e. *Peyssonnelia* spp. and *L. pustulatum*) were more abundant on higher outcrops (Type 2). Inshore, where the depth ranges from 10 to 15 m, the highest outcrops seemed to be less stressed by the resuspension of sediments caused by waves and winds compared to the lower ones.

Given the complex physico-chemical and trophic conditions in the northern Adriatic, it is conceivable that the higher elevation of the outcrops has the same effect on the macroalgae as the distance from the coast, especially regarding sedimentation and resuspension of sediments. On the contrary, offshore the outcrops height did not have a significant role in structuring the macroalgal assemblages.

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Authors' addresses:
D. Curiel, C. Miotti, E. Checchin, A. Rismondo - SELC, Via dell'Elettricità 3/d, I-30175 Venezia-Marghera, Italy; Curiel@selc.it
S. Kaleb, A. Falace - Università degli Studi di Trieste, Dipartimento di Scienze della Vita, Via L. Giorgieri 10, I-34127 Trieste, Italy