

Invasions of alien macroalgae in Mediterranean coralligenous assemblages

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Abstract – In this study, a combination of univariate and multivariate analysis was used to compare macroalgal assemblages of Mediterranean coralligenous system in areas invaded by the alien species *Caulerpa racemosa* var. *cylindracea* and *Womersleyella setacea* with reference assemblages. Results showed that assemblages strongly differed between invaded and reference areas in relation to both assemblage structure and species richness. Moreover, significant differences were detected between assemblages colonized by different invaders: *C. racemosa* var. *cylindracea* seemed to affect mostly encrusting organisms, while turf algae decreased in areas invaded by *W. setacea*. The present study showed that invasions of alien macroalgae could represent a serious threat for Mediterranean coralligenous assemblages.

biological invasions / *Caulerpa racemosa* var. *cylindracea* / coralligenous assemblages / Mediterranean Sea / subtidal / *Womersleyella setacea*

Résumé – Invasions de macroalgues exotiques dans les peuplements algaux coralligènes méditerranéens. Des peuplements algaux coralligènes méditerranéens dans des aires envahies par les algues exotiques *Caulerpa racemosa* var. *cylindracea* et *Womersleyella setacea* ont été comparés avec des peuplements de référence en utilisant des méthodes uni-variées et multi-variées. Les résultats ont montré que les peuplements envahis montraient des différences quant à la structure et au nombre d'espèces. En outre, des différences significatives ont été trouvées entre les peuplements colonisés par les deux espèces envahissantes: *C. racemosa* var. *cylindracea* endommage surtout les espèces encroûtantes, tandis que les espèces gazonnantes sont surtout réduites dans les aires envahies par *W. setacea*. La présente étude a montré que les invasions par des algues exotiques peuvent représenter une menace pour les peuplements coralligènes méditerranéens.

Invasions biologiques / *Caulerpa racemosa* var. *cylindracea* / peuplements coralligènes / Mer Méditerranée / subtidal / *Womersleyella setacea*

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INTRODUCTION

Deep subtidal rocky habitats of the Mediterranean Sea are characterised by assemblages dominated by calcareous organisms, defined as “coralligenous” (Pérès & Picard, 1964). This system is characterised by a high species diversity (Hong, 1982; Laborel, 1987) that is enhanced by environmental stability and by a prevalence of biotic factors that support the distribution of sessile organisms. Moreover, in this system heterogeneity of the rocky bottom is increased by a complex microtopography related to the development of a secondary substratum provided by builder organisms, mostly calcareous algae. This high heterogeneity of the substratum promotes the presence of a high number of species per unit area (Cocito, 2004; Ballesteros, 2006). As other marine and terrestrial habitats characterised by high diversity related to the stability of physical factors and regulated by biotic interactions, coralligenous assemblages are sensitive to impact, especially if caused by human activities (Hong, 1983). The effects of physical factors on coralligenous assemblages have been investigated (Balata *et al.*, 2005); however, little is known about the influence of biological disturbance on these systems. Biological pollution caused by invasions of introduced species is considered a major threat to biodiversity in marine habitats (Walker & Kendrick, 1998). However, no studies have been conducted on the effect of introduced species in deep subtidal assemblages.

In the Mediterranean Sea, invasions of exotic macroalgae have caused serious ecological problems in coastal areas (Verlaque, 1994; Boudouresque & Verlaque, 2002). Biological invasions of *Caulerpa* species and filamentous Rhodophyta are considered particularly serious. The red alga *Womersleyella setacea* (Hollenberg) R.E. Norris is the most widespread filamentous seaweed introduced in the Mediterranean Sea and it is able to produce dense turfs that cover other benthic organisms (Airoldi *et al.*, 1995; Piazzi & Cinelli, 2000, 2001). *Caulerpa racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman *et al.* Boudouresque represents one of the most significant invasions in the Mediterranean Sea, showing wide colonization across the whole basin (Verlaque *et al.*, 2003; Piazzi *et al.*, 2005b). These algae are strong competitors that interfere with native assemblages (Airoldi, 1998; Piazzi *et al.*, 2001; Piazzi & Cinelli, 2003). The effects of the invasion of these two seaweeds have been widely studied in Mediterranean subtidal rocky habitats, where strong structural modifications and a severe decrease in species diversity have been observed in the assemblages invaded (Airoldi *et al.*, 1995; Airoldi & Virgilio, 1998; Piazzi & Cinelli, 2000, 2003; Piazzi *et al.*, 2001; Balata *et al.*, 2004). However, no studies have investigated the structure and composition of assemblages invaded by alien species in coralligenous systems, even though invasion by *W. setacea* has been documented for this type of community (Piazzi *et al.*, 2004b). Despite this lack of information, it is reasonable to suppose that coralligenous systems can be potentially more sensitive than shallow assemblages to invasion of species, such as *C. racemosa* var. *cylindracea* and *W. setacea*, which are able to thrive in depths greater than 50 m (Piazzi *et al.*, 2004a, 2005b).

The aim of this study was to describe the structure of coralligenous communities in areas invaded by alien species and to compare them with native, unaffected assemblages. A combination of multivariate and univariate analysis was used to test the hypothesis that invaded and uninvaded assemblages differed in composition, structure and species diversity.

MATERIALS AND METHODS

The study was carried out along the Tuscany coast (43°28'24" N, 10° 19'42" E) on a reef at about 30 m of depth. This site has been invaded by *Womersleyella setacea* since the early 1990s (Airoldi *et al.*, 1995), whereas *Caulerpa racemosa* var. *cylindracea* been spreading in the zone since 2004. Areas dominated by turfs or by *C. racemosa* var. *cylindracea* are patchily distributed. The study was carried out in October 2005, a time of the year in which both *C. racemosa* var. *cylindracea* and *W. setacea* are in the phase of their maximal vegetative development (Airoldi *et al.*, 1995; Piazzini & Cinelli, 1999).

Three different conditions were selected: patches dominated by *C. racemosa* var. *cylindracea*, patches dominated by turfs and reference zones. Two areas (2 m × 10 m) were randomly chosen for each condition; areas ascribed to different conditions were selected with interspersed arrangement. In each area, 3 replicated samples were collected by scraping a 400 cm² surface from the bottom. Materials were preserved in 4% formalin seawater and observed under a binocular microscope to identify macroalgal species and evaluate the cover of each species. The cover of a species was estimated as the surface covered by the vertical projection of the alga and expressed as the percentage of sampling area (Boudouresque, 1971). Total percentage cover was calculated for each sample by summing the percentage cover of all the algae in the sample. Species richness of each sample was counted. To describe macroalgal assemblages, percentage cover was also separately estimated for encrusting, erect and turf layers (Airoldi *et al.*, 1995).

Non-parametric multivariate analysis of variance (PERMANOVA, Anderson, 2001) based on permutations was used to test the hypothesis that macroalgal assemblages differed among the three conditions examined. Bray-Curtis dissimilarities for this analysis were calculated using untransformed data. The analysis consisted of a 2-way model with Condition (3 levels: *C. racemosa* var. *cylindracea*; *W. setacea*; reference) as a fixed factor and Area (2 levels) as random factor nested within Condition. Monte Carlo procedures were used to calculate probability when possible permutations were not enough to get a reasonable test (Anderson, 2001). The number of permutation units is reported in Table 2. For graphical representation of the data, a two-dimensional metric multidimensional scaling (MDS) ordination based on centroids of the factor Condition was carried out. The program IndVal (Indicator Values) was used to determine which species were responsible for the possible differences between the three Conditions (Dufrene & Legendre, 1997).

Species richness, total percentage cover and percentage cover of vegetation layers were analysed by a 2-way ANOVA, utilizing the same factors and levels 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). Percentage cover of turf layer did not include values of abundance of *W. setacea*.

RESULTS

A total of 64 macroalgal species were found: 7 Chlorophyta, 7 Phaeophyceae and 49 Rhodophyta (Table 1, with nomenclature authority). In reference areas, the encrusting layer was well developed and formed by encrusting corallines,

Table 1. List of taxa with the mean percentage cover. R = reference areas, C = areas invaded by *Caulerpa racemosa* var. *cylindracea*, W = areas invaded by *Womersleyella setacea*.

TAXA	R	C	W
ENCRUSTING LAYER			
Chlorophyta			
<i>Palmophyllum crassum</i> (Naccari) Rabenhorst	0.17	–	–
<i>Valonia macrophysa</i> Kützing	0.02	0.03	–
Phaeophyceae			
<i>Zanardinia typus</i> (Nardo) G. Furnari	1.47	0.95	–
Rhodophyta			
<i>Contarinia squamariae</i> (Meneghini) Denizot	0.27	0.02	–
Encrusting corallinaceae	100.0	40.83	100.0
<i>Peyssonnelia rubra</i> (Greville) J. Agardh	9.58	1.75	8.33
TURF LAYER			
Chlorophyta			
<i>Cladophora echinus</i> (Biasoletto) Kützing	–	0.03	–
<i>Cladophora prolifera</i> (Roth) Kützing	0.08	2.48	0.23
<i>Pseudochlorodesmis furcellata</i> (Zanardini) Børgesen	0.65	–	–
Phaeophyceae			
<i>Dictyota linearis</i> (C. Agardh) Greville	0.68	0.92	0.78
<i>Sphacelaria cirrosa</i> (P.H. Roth) C. Agardh	0.32	0.05	0.47
<i>Sphacelaria plumula</i> Zanardini	–	0.02	–
Rhodophyta			
<i>Acrothamnion preissii</i> (Sonder) Wollaston	0.13	0.33	0.18
<i>Aglaothamnion tenuissimum</i> (Bonnemaison) Feldmann-Mazoyer	0.57	0.07	0.35
<i>Aglaothamnion tripinnatum</i> (C. Agardh) Feldmann-Mazoyer	0.02	–	–
<i>Antithamnion cruciatum</i> (C. Agardh) Nägeli	0.62	0.50	0.07
<i>Antithamnion tenuissimum</i> (Hauck) Schiffner	0.02	–	–
<i>Apoglossum ruscifolium</i> (Turner) J. Agardh	0.38	0.02	–
<i>Ceramium cimbricum</i> H.E. Petersen	0.08	0.07	0.22
<i>Ceramium circinatum</i> (Kützing) J. Agardh	0.03	–	–
<i>Ceramium codii</i> (H. Richards) Feldmann-Mazoyer	0.05	–	0.02
<i>Ceramium flaccidum</i> (Kützing) Ardissonne	0.07	0.03	0.05
<i>Champia parvula</i> (C. Agardh) Harvey	0.30	0.12	0.12
<i>Chondria dasyphylla</i> (Woodward) C. Agardh	0.88	0.07	–
<i>Chondria capillaris</i> (Hudson) M.J. Wynne	0.03	0.02	–
<i>Crouania attenuata</i> (C. Agardh) J. Agardh	0.18	0.05	0.17
<i>Dasya ocellata</i> (Grateloup) Harvey	–	–	–
<i>Dasya rigidula</i> (Kützing) Ardissonne	–	–	–
<i>ErythroGLOSSUM sandrianum</i> (Kützing) Kylin	0.02	0.05	–
<i>Eupogodon planus</i> (C. Agardh) Kützing	0.12	0.57	0.73
<i>Falkenbergia rufolanosa</i> (Harvey) F. Schmitz stadium	0.93	0.17	0.07
sporophyte of <i>Asparagopsis armata</i> Harvey			
<i>Feldmannophycus rayssiae</i> (Feldmann & Feldmann-Mazoyer) Augier & Boudouresque	0.38	0.57	0.87
<i>Jania adhaerens</i> J.V. Lamouroux	2.78	5.87	0.58
<i>Halydictyon mirabile</i> Zanardini	0.12	0.02	–
<i>Herposiphonia secunda</i> (C. Agardh) Ambronn	0.10	–	–
<i>Heterosiphonia crispella</i> (C. Agardh) M.J. Wynne	0.80	0.45	0.03

Table 1. List of taxa with the mean percentage cover. R = reference areas, C = areas invaded by *Caulerpa racemosa* var. *cylindracea*, W = areas invaded by *Womersleyella setacea*. (continued)

TAXA	R	C	W
<i>Hypoglossum hypoglossoides</i> (Stackhouse) Collins & Harvey	0.08	0.03	0.37
<i>Lomentaria chyoclaadiella</i> Funk	0.18	–	0.15
<i>Monosporus pedicellatus</i> (J.E. Smith) Solier	0.05	0.02	–
<i>Nitophyllum</i> sp.	0.18	–	0.12
<i>Plocamium cartilagineum</i> (Linnaeus) P.S. Dixon	0.22	0.83	–
<i>Polysiphonia elongata</i> (Hudson) Sprengel	–	0.18	–
<i>Polysiphonia furcellata</i> (C. Agardh) Harvey	–	0.03	0.63
<i>Polysiphonia perforans</i> Cormaci, G. Furnari, Pizzuto & Serio	0.03	–	–
<i>Ptilothamnion pluma</i> (Dillwyn) Thuret	0.17	0.02	0.05
<i>Rhodophyllis divaricata</i> (Stackhouse) Papenfuss	0.18	–	0.10
<i>Rodriguezella strafforelloii</i> F. Schmitz	0.24	0.12	0.32
<i>Spyridia filamentosa</i> (Wulfen) Harvey	–	1.45	–
<i>Wrangelia penicillata</i> (C. Agardh) C. Agardh	1.17	0.17	0.03
ERECT LAYER			
Chlorophyta			
<i>Flabellia petiolata</i> (Turra) Nizamuddin	44.08	2.92	11.00
<i>Halimeda tuna</i> (J. Ellis & Solander) J.V. Lamouroux	5.33	–	2.67
Phaeophyceae			
<i>Cystoseira spinosa</i> Sauvageau	0.05	–	–
<i>Halopteris filicina</i> (Grateloup) Kützing	1.63	0.57	0.35
<i>Nereia filiformis</i> (J. Agardh) Zanardini	–	0.02	–
Rhodophyta			
<i>Acrodiscus vidovichii</i> (Meneghini) Zanardini	0.33	–	0.22
<i>Amphiroa cryptarthrodia</i> Zanardini	0.73	0.22	–
<i>Botryocladia botryoides</i> (Wulfen) Feldmann	0.30	0.20	0.53
<i>Gelidium bipectinatum</i> G. Furnari	0.17	0.33	0.08
<i>Halopithys incurva</i> (Hudson) Batters	–	4.08	–
<i>Meredithia microphylla</i> (J. Agardh) J. Agardh	0.73	1.28	0.60
<i>Osmundea pelagosae</i> (Schiffner) F.W. Nam	12.78	8.77	5.50
<i>Sphaerococcus coronopifolius</i> Stackhouse	0.25	–	–
<i>Tricleocarpa fragilis</i> (Linnaeus) Huisman & R.A. Townsend	2.12	1.00	0.17

Peyssonnelia rubra and *Zanardina typus*. The most abundant erect species were *Flabellia petiolata*, *Halimeda tuna*, *Osmundea pelagosae* and *Tricleocarpa fragilis*. The most common species in the turf were *Pseudochlorodesmis furcellata*, *Dictyota linearis*, *Chondria dasyphylla*, *Asparagopsis armata* (*Falkenbergia rufolanosa* phase), *Jania adhaerens*, *Heterosiphonia crispella* and *Wrangelia penicellata*. *Caulerpa racemosa* var. *cylindracea* and *Womersleyella setacea* showed values of percentage cover of 100 in the areas selected as invaded by these algae (Fig. 1).

PERMANOVA analyses detected significant differences in the structure of assemblages in relation to Condition and Area (Table 2). Metric MDS ordination showed a clear separation between reference areas and invaded areas; furthermore, areas invaded by *C. racemosa* var. *cylindracea* were separated from those invaded by *W. setacea* (Fig. 2).

Table 2. Results of PERMANOVA on the structure of assemblages. Significant effects are indicated in bold.

Source	df	MS	pseudoF	P	P(MC)	Denominator	N° permutation units
Condition = Co	2	4198.59	11.96	0.075	0.006	Ar(Co)	6
Area(Co) = Ar(Co)	3	350.95	3.37	0.052	0.033	Res	18
Residual = Res	12	104.02					
Total	17						

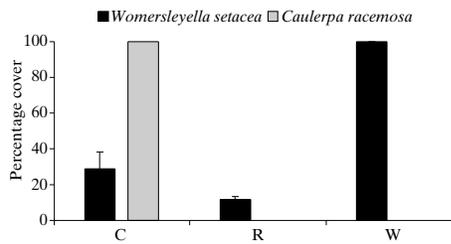


Fig. 1. Percentage cover of *Caulerpa racemosa* var. *cylindracea* and *Womersleyella setacea* in the studied assemblages. C = areas invaded by *C. racemosa* var. *cylindracea*, W = areas invaded by *W. setacea*, R = reference areas.

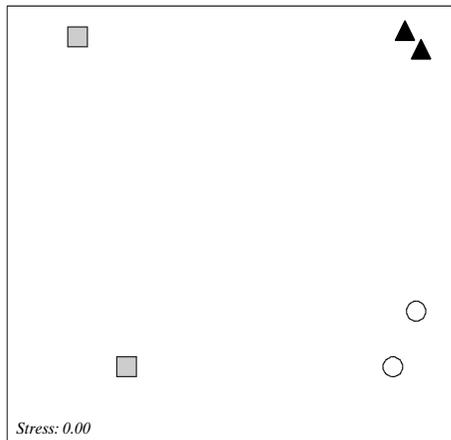


Fig. 2. Metric MDS ordination based on Bray-Curtis dissimilarity coefficient applied to species-samples matrix. Squares = *Caulerpa racemosa* var. *cylindracea* areas, triangles = *Womersleyella setacea* areas, circles = reference areas.

In areas invaded by *Caulerpa racemosa* var. *cylindracea*, the IndVal analysis (Table 3) showed that erect species, such as *Halimeda tuna*, and turf species, such as *Pseudochlorodesmis furcellata*, *Apoglossum ruscifolium* and *Chondria dasyphylla*, were lower in abundance, while *Cladophora prolifera* and *Halopithys incurva* were higher in terms of percentage cover. In areas invaded by *Womersleyella setacea*, several turf species widely distributed in control areas were absent or showed lower cover values (*Pseudochlorodesmis furcellata*, *Apoglossum ruscifolium*, the *Falkenbergia* phase of *Asparagopsis armata*, *Chondria dasyphylla*, *Heterosiphonia crispella*, *Wrangelia penicillata*).

Table 3. Results of the Indicator Species Analysis (IndVal). Numbers indicate cases (number of replicates out of six) where each taxon is significantly different in abundance (A) and/or presence (P); R: reference areas, C: areas invaded by *Caulerpa racemosa*, W: areas invaded by *Womersleyella setacea*.

References vs <i>Caulerpa racemosa</i>		References vs <i>Womersleyella setacea</i>		Womersleyella setacea vs <i>Caulerpa racemosa</i>	
R A P	C A P	R A P	W A P	W A P	C A P
4/6	0/0	4/6	0/0	0/0	25/6
	<i>Pseudochlorodesmis furcellata</i>		<i>Pseudochlorodesmis furcellata</i>		<i>Halopithys incurva</i>
1/6	0/0	2/6	0/0	0/2	3/6
	<i>Nitophyllum</i> sp.		<i>Apoglossum ruscifolium</i>		<i>Heterosiphonia crispella</i>
32/6	0/0	5/6	0/0	1/3	15/6
	<i>Halimeda tuna</i>		<i>Chondria dasyphylla</i>		<i>Cladophora prolifera</i>
2/6	0/1	7/6	0/1		
	<i>Apoglossum ruscifolium</i>		<i>Wrangelia penicillata</i>		
5/6	0/3	5/6	0/2	16/6	0/0
	<i>Chondria dasyphylla</i>		<i>Heterosiphonia crispella</i>		<i>Halimeda tuna</i>
3/6	0/4	9/5	0/0	4/6	0/1
	<i>Aglaohammion tenuissimum</i>		<i>Zanardina typus</i>		<i>Polysiphonia furcellata</i>
7/6	1/3	1/5	0/0	2/6	0/2
	<i>Wrangelia penicillata</i>		<i>Plocamium cartilaginum</i>		<i>Hypoglossum hypoglossoides</i>
1/5	0/0	4/5	0/0	3/6	0/3
	<i>Rodophyllis divaricata</i>		<i>Amphiroa cryptarthrodia</i>		<i>Sphacelaria cirrosa</i>
1/6	0/3	10/6	2/2	2/6	0/4
	<i>Crouania attenuata</i>		<i>Halopteris flicina</i>		<i>Aglaohammion tenuissimum</i>
2/5	0/3	6/5	0/1	1/4	0/0
	<i>Contarina squamariae</i>		<i>Falkenbergia rufutanosa</i>		<i>Nitophyllum</i> sp.
1/4	0/1			1/4	0/0
	<i>Ptilohammion pluma</i>				<i>Acrodiscus vodovichii</i>
0/0		0/0	4/6	1/3	0/0
	<i>Halopithys incurva</i>		<i>Polysiphonia furcellata</i>		<i>Lomentaria chylocladiella</i>
1/1		1/3	2/6		
	<i>Cladophora prolifera</i>		<i>Hypoglossum hypoglossoides</i>		
		25/6		15/6	

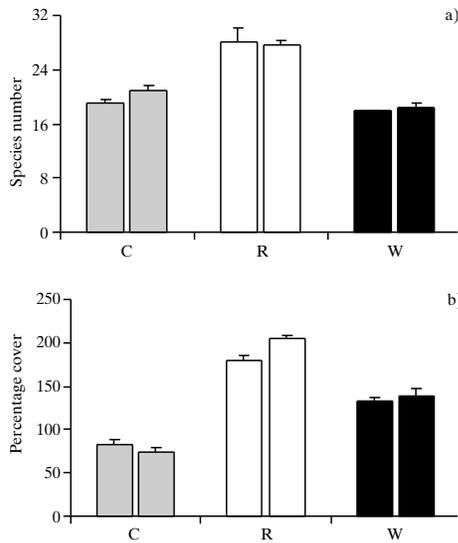


Fig. 3. Species number and total percentage cover of macroalgal assemblages (means + SE, n=3). C = areas invaded by *Caulerpa racemosa* var. *cylindracea*, W = areas invaded by *Womersleyella setacea*, R = reference areas.

Table 4. Results of 2-way ANOVA on total percentage cover and species number of macroalgal assemblages. Significant values are written in bold. R = reference areas, C = areas invaded by *Caulerpa racemosa* var. *cylindracea*, W = areas invaded by *Womersleyella setacea*.

Source of variation	df	Total percentage cover			Species number		
		Ms	F	P	Ms	F	P
Condition = C	2	19694.63	54.41	0.004	0.273	58.20	0.004
Areas (C)	3	361.95	4.2	0.030	0.005	1.04	0.411
Residual	12	86.14			0.005		
Cochran's C			0.469			0.548	
Transformation			none			Ln (x+1)	
SNK test			R > W > C			R > W = C	
S. E.:			7.76			0.03	

The species number per sample area ranged between 28.0 ± 2.1 (mean \pm SE; n = 3) in reference assemblages and 18.3 ± 0.8 in assemblages invaded by *W. setacea* (Fig. 3a). Total percentage cover ranged between 180.6 ± 4.5 in reference assemblages and 73.3 ± 5.1 in assemblages invaded by *C. racemosa* var. *cylindracea* (Fig. 3b). ANOVA analysis detected significant differences among Conditions in relation to both the total percentage cover and the species number (Table 4); the SNK test showed that reference areas had values significantly higher for both the variables and *W. setacea* areas had values of total percentage cover higher than those of *C. racemosa* var. *cylindracea* areas.

In reference assemblages, the mean percentage cover of vegetation layers was 112.7 ± 5.0 for encrusting algae, 13.8 ± 2.7 for turf species and 83.0 ± 4.5 for

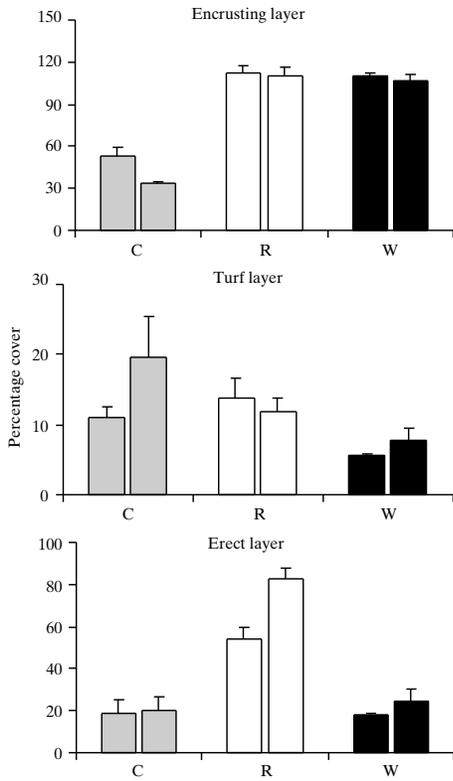


Fig. 4. Percentage cover of vegetation layers (means + SE, n=3). C = areas invaded by *Caulerpa racemosa* var. *cylindracea*, W = areas invaded by *Womersleyella setacea*, R = reference areas.

Table 5. Results of 2-way ANOVA on percentage cover of encrusting, turf and erect layers of macroalgal assemblages. Significant values are written in bold. R = reference areas, C = areas invaded by *Caulerpa racemosa* var. *cylindracea*, W = areas invaded by *Womersleyella setacea*.

Source of variation	df	Encrusting layer			Turf layer			Erect layer		
		MS	F	P	Ms	F	P	MS	F	P
Condition = C	2	8806.42	44.03	0.006	0.84	5.83	0.092	4663.84	10.61	0.043
Areas (C) = A	3	200.02	3.12	0.066	0.14	1.56	0.249	439.72	5.15	0.016
Residual	12	64.17			0.09			85.40		
Cochran's C			0.303			0.417			0.247	
Transformation			none			Ln (x+1)			none	
SNK test			R = W > C			R = W = C			R > W = C	
S. E.:			5.77			0.15			8.56	

erect species (Fig. 4). ANOVA analysis showed significant differences among conditions for the percentage cover of encrusting and erect layers, while no significant differences were detected for the percentage cover of turf layer (Table 5). The SNK test showed that the percentage cover of the erect layer was

higher in reference assemblages than in invaded assemblages, while the encrusting layer in assemblages invaded by *C. racemosa* var. *cylindracea* showed cover values lower than those of the other assemblages (Table 5, Fig. 4).

There was significant variability between areas for total percentage cover and for percentage cover of erect species.

DISCUSSION

The results of this study showed that assemblages strongly differed between invaded and reference areas in relation to both assemblage structure and species richness. Furthermore, significant differences were detected between assemblages colonized by different invaders.

Differences detected between reference and invaded assemblages are similar to those described for shallower rocky assemblages for both *Womersleyella setacea* (Airoldi *et al.*, 1995; Airoldi, 1998) and *Caulerpa racemosa* var. *cylindracea* (Piazzì *et al.*, 2001). Invaded assemblages showed lower species richness and percentage cover of macroalgae; moreover, erect species were less abundant in both invaded assemblages. Erect species reproduce primarily sexually and for this reason they can be affected by invaders that constitute wide mats on the substrate, preventing the establishment of spores, zygotes and other propagules of native species (Airoldi, 2000b). The pre-emption of the substratum can be considered the most important competitive mechanism of species such as *C. racemosa* var. *cylindracea* and *W. setacea*, which grow in thick mats that persist for long periods of time (Airoldi, 1998; Piazzì & Ceccherelli, 2006). The capability of these seaweeds of trapping sediments further enhances this competitive mechanism (Airoldi & Virgilio, 1998; Piazzì *et al.*, 2005a), making the effects of both invasions more serious and persistent.

Although the two invaders showed many similar competitive traits, differences in invaded assemblages were detected. *C. racemosa* var. *cylindracea* seemed to affect mostly encrusting organisms, while turfs were most affected in areas invaded by *W. setacea*. The mechanisms concerned in the co-occurrence of encrusting species and *W. setacea* have been widely studied. The respective abilities of turfs and crusts to overgrow and tolerate overgrowth minimizes the importance of competition and allows the coexistence of these algae as dominant forms in benthic assemblages (Airoldi, 2000a). Conversely, mats constituted by *C. racemosa* var. *cylindracea* stolons seem to affect strongly the lower vegetation layers, both encrusting and epilithic species. Mats formed by stolons are thicker than those of turfs, preventing light penetration, trapping sediments and creating a reduced habitat on the substratum covered.

Turf species seem to suffer the competition with *W. setacea*. This alga is a strong competitor, because it is able to eliminate species with a similar ecological niche. Although interactions among turf species are not investigated, mechanisms as vegetative reproduction, faster growth, better exploitation of nutrients or ability to trap sediments (Carpenter, 1990) may be involved in the capability of *W. setacea* of monopolizing the substratum. Most filamentous species occurring in the assemblages studied were characterised by sexual reproduction and vertical development of the thallus; thus, they needed bare substratum where spores and zygotes could settle. Conversely, Mediterranean *W. setacea* reproduces only by vegetative fragmentation (Rindi *et al.*, 1999) and spread through prostrate

axes. While recruitment by sexual propagules can be highly variable in space and time and influenced by environmental conditions, spread by vegetative reproduction is presumably more constant, contributing to the persistent dominance of the species reproducing with this mechanism. Vegetative reproduction, together with the capability of prostrate axes of *W. setacea* to spread on all types of substratum and on other organisms, enhance the competitiveness of this species against other Mediterranean turf-algae. In ecological studies, the knowledge of the species composition within each algal layer is important, in order to distinguish patterns due to the single species from those due to all the species of the layer.

This correlative study does not allow the establishment of a cause-effect relationship between invaders and the described structure of assemblages. However, the similarity between our results and results of studies in shallower assemblages (Piazzi *et al.*, 2001; Airoidi, 2003) showed that invader abundance may be responsible for the differences between the assemblages examined. Further studies are needed to investigate the effects of invaders on coralligenous assemblages, in order to obtain information about this phenomenon at larger spatial scales and for long periods. Moreover, manipulative studies should be performed to investigate mechanisms involved in the competition between invaders and coralligenous species, both algae and sessile animals. In fact, these latter represent an important component of coralligenous systems, also contributing to the building of calcareous structures (Cocito, 2004) and they could be negatively influenced by overgrowth of species such as *C. racemosa* var. *cylindracea* and *W. setacea*.

The present study, although related to a single zone, showed that macroalgal invasions can negatively affect coralligenous rocky assemblages, as already demonstrated for other Mediterranean marine habitats (Verlaque & Fritayre, 1994; Boudouresque & Verlaque, 2002; Piazzi & Cinelli, 2003). Coralligenous assemblages represent Mediterranean biodiversity hotspots; therefore, invaders pose significant threats to the whole littoral system. Biological invasions interact with changes in environmental conditions that affect this system (Balata *et al.*, 2005, 2006), causing ecological modifications on large-scale and severe economical consequences.

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