

Sediment as a constituent of Mediterranean benthic communities dominated by *Caulerpa racemosa* var. *cylindracea*

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SUMMARY: Mediterranean macroalgal assemblages in areas invaded and non-invaded by *Caulerpa racemosa* var. *cylindracea* were compared and trapped sediments were characterised. Results showed that assemblages invaded by *C. racemosa* var. *cylindracea* differed greatly from non-invaded ones: encrusting and erect algae, both articulated and foliose, decreased in invaded areas, while opportunistic filamentous species increased their abundance. The percentage of sediment was 7 times higher in areas invaded by *C. racemosa* var. *cylindracea* than in non-invaded areas. Characteristics of trapped sediments were similar in all the studied assemblages, while redox values were lower in the invaded ones. Results suggested that sediment constitutes an important component in *C. racemosa* var. *cylindracea* populations, probably enhancing the competitive ability of this species.

Keywords: biological invasions, *Caulerpa racemosa*, macroalgal assemblages, Mediterranean Sea, sediments.

RESUMEN: EL SEDIMENTO COMO CONSTITUYENTE DE COMUNIDADES BENTÓNICAS MEDITERRÁNEAS DOMINADAS POR *CAULERPA RACEMOSA* VAR. *CYLINDRACEA*. – Las comunidades de macroalgas mediterráneas en áreas invadidas por *C. racemosa* var. *cylindracea* y áreas no invadidas fueron comparadas y el sedimento retenido caracterizado. Los resultados muestran que las áreas invadidas por *C. racemosa* var. *cylindracea* difieren de forma marcada de las poblaciones no invadidas: algas incrustantes y erectas, articuladas y foliosas, decrecen en las áreas invadidas, mientras que las especies filamentosas oportunistas aumentan su abundancia. El porcentaje de sedimento fue siete veces mayor en áreas invadidas por *C. racemosa* var. *cylindracea* que en áreas no invadidas. Las características del sedimento atrapado fueron similares en todas las poblaciones estudiadas, mientras que los valores del potencial redox fueron menores en las zonas invadidas. Nuestros resultados sugieren que el sedimento constituye un componente importante en las poblaciones de *C. racemosa*, var. *cylindracea*, posiblemente aumentando la capacidad competitiva de esta especie.

Palabras clave: invasiones biológicas, *Caulerpa racemosa*, comunidades macroalgales, Mediterráneo, sedimentos.

INTRODUCTION

Physical and biological factors interact to determine the temporal and spatial distribution of benthic marine assemblages, making it difficult to understand mechanisms of community regulation (Schiel and Forster, 1986; Paine, 1990; Lüning, 1993; Middelboe *et al.*, 1997; Baynes, 1999). In fact, the

effects of physical factors can strongly modify the results of interspecific interactions, such as competition or predation (Underwood and Jernakoff, 1984; Andrew and Viejo, 1998; Kaehler and Williams, 1998; Benedetti-Cecchi *et al.*, 2000). In coastal areas, sedimentation may be considered one of the most important physical factors affecting benthic communities (Airoldi, 2003).

Sediments can influence benthic assemblages through several mechanisms. The disturbance caused by burial and smothering can damage a great number of benthic taxa, favouring the spread of tolerant and opportunistic species (Irving and Connell, 2002a, b; Eriksson and Johansson, 2003; Balata *et al.*, 2005). On the other hand, the ability of some species to trap sediments can enhance their spread, avoiding predation and favouring their competitiveness (Airoldi, 2003). The latter mechanism has been widely studied in relation to turf-forming algae (Kendrick, 1991; Airoldi *et al.*, 1996) and it has been observed to increase the invasiveness of introduced filamentous species such as the Rhodophyta *Womersleyella setacea* (Hollenberg) R.E. Norris (Airoldi and Cinelli, 1997). However, the importance of sediment trapping in ecological regulation of other benthic assemblages is less known, although this mechanism has been suggested to play a key role in the competitiveness of invasive algal species (Verlaque and Fritayre, 1994).

Caulerpa racemosa (Forsskål) C. Agardh var. *cylindracea* (Sonder) Verlaque, Huisman *et Boudouresque* (Verlaque *et al.*, 2003) (hereafter *Caulerpa racemosa*) represents a serious threat for native benthic communities in the Mediterranean Sea, affecting biodiversity and habitat complexity (Piazzini *et al.*, 2005a). The interaction between *C. racemosa* and sediments has recently been investigated, showing that the alga is tolerant to high sedimentation rates and suggesting that its competitiveness could be enhanced by the ability to trap sediments (Piazzini *et al.*, 2005b). However, limited information is available on the role of sediments in Mediterranean populations of *C. racemosa*.

The aim of the present study is to advance knowledge on interactions between sediments and *C. racemosa*. In particular, we tested the hypothesis that there were differences between invaded and non-invaded areas in i) the composition of species and morphological forms of Mediterranean shallow rocky assemblages, ii) the amount and quality of sediment trapped by the assemblages and iii) the ratio between the amount of sediment and biomass.

MATERIAL AND METHODS

The study was carried out in the northwestern Mediterranean Sea, along the coasts of Tuscany (43°30'N, 10°20'E). It was conducted at 3 m depth

on rocky bottoms invaded by *Caulerpa racemosa* since 1996 (Piazzini *et al.*, 1997). The alga showed a patchy distribution, with well developed mats in invaded patches.

In the study area, 2 sites invaded by *C. racemosa* and 2 non-invaded sites interspersed among them were randomly chosen. The sites were 4 m² wide and at least 20 metres apart. In November 2004, at the end of vegetative growth of the alga (Ruitton *et al.*, 2005), 3 replicated samples were collected at each site. Samples comprised macroalgae and trapped sediment, and were collected by scraping 400 cm² of substrate with hammer and chisel. Before scraping, the sediment trapped and deposited over the assemblages within each sampling surface was collected by using a suction pump to avoid the loss of the finest fractions during sampling (Balata *et al.*, 2005).

Macroalgae were identified under the microscope. Cover of each species was estimated as vertical projection of the alga and expressed as the percentage of the sampling surface (Boudouresque, 1971). Macroalgal species were lumped into morphological groups according to Steneck and Dethier (1994) (foliose, filamentous, corticated terete, crustose, articulated) and the percentage cover of each group was calculated as the sum of the percentage cover of all the algae belonging to the group. Biomass of *C. racemosa* and macroalgae was evaluated as dry weight after 48 h at 60°C.

Multivariate (PERMANOVA) and univariate (ANOVA) procedures were used to test for differences between invaded and non-invaded sites.

PERMANOVA based on permutations was used to test the hypothesis that benthic assemblages invaded by *C. racemosa* differed in composition and relative abundance from the non-invaded ones (Anderson, 2001a, b). Bray-Curtis dissimilarities for this analysis were calculated on untransformed data. The permutable units and the Mean Square (MS) used as the denominator for each source of variability are reported in Table 1. The analysis consisted of a 2-way model with Invasion (invaded vs. non-invaded assemblages) as the fixed factor and Site (2 levels) as the random factor nested in Invasion. The amount of sediment was used as a covariable in the analysis to test possible relationships with the assemblage.

The IndVal (Indicator Value) program was used to identify the species or morphological groups that contributed most to the differences between invaded and non-invaded sites. This method was preferred to

TABLE 1. – Results of PERMANOVA on the species composition and abundance of assemblages. Significant effects are indicated in bold. P(MC): P values obtained through Monte Carlo methods

Source	df	MS	Pseudo-F	P	P (MC)	Denominator	N° perm. units
Sediment (Covariable)	1	14381.30	23.93	0.003			
Invasion = (In)	1	4953.13	10.28	0.955	0.007	Si(In)	4
Site (In) = Si(In)	2	481.70	0.80	0.675	0.641	Res	12
Residual = Res	8	600.96					
Total	11						

others because it combines the relative abundances of species with their relative frequencies in the groups of samples (Dufrene and Legendre, 1997). The indicator species are defined as the most characteristic species of each group, found mostly in a single group and present in the majority of the samples belonging to that group.

Data of algal biomass, species number and percentage cover of morphological groups were analysed using analysis of variance (ANOVA). Factors and levels in these analyses were the same as in the multivariate analysis. Cochran's C-test was utilised before each analysis to check for homogeneity of variance and data were transformed when necessary. In cases of unresolvable heterogeneous variances, analyses were run on untransformed data (Underwood, 1997).

Sediment was separated from algae and redox potential was measured at 1 cm depth using an Eh-electrode (Orion 250 A) connected to an mV meter within one hour after sampling. The amount of sediment was evaluated as dry weight obtained after filtration, elimination of organic matter in H₂O₂ for 72 h and drying for 48 h at 60°C (Airoldi *et al.*, 1996). Sediment weight was analysed by analysis of vari-

ance (ANOVA) using the same factors and levels described above. Optical microscope analysis was performed on all the samples. X-ray powder diffractions were carried out on all the sediments to identify the mineralogical composition.

RESULTS

PERMANOVA showed significant differences between non-invaded and invaded assemblages, which were consistent between sites (Table 1). The IndVal analysis showed that algal species characterising the invaded sites were *Cladophora prolifera*, *Hypnea musciformis*, *Ceramium circinatum*, *Spyridia filamentosa* and *Plocamium cartilagineum*, while several erect (*Halimeda tuna*, *Padina pavonica*, *Laurencia obtusa*, *Dictyopteris polypodioides*) and encrusting coralline algae were abundant at non-invaded sites and absent at invaded sites (Table 2).

The biomass of macroalgae other than *Caulerpa racemosa* was 453.7±39.5 g m⁻² (mean±SE, n=6) at non-invaded sites and 227.5±5.7 g m⁻² at sites invaded by *C. racemosa* (Fig. 1a). The biomass of *C. racemosa* at invaded sites was 105.0±5.6 g m⁻². The

TABLE 2. – Results of the Indicator Species Analysis (IndVal). Numbers indicate cases (numbers of samples out of 6) in which each taxon is significantly different in abundance (A) or presence (P) between invaded and non-invaded areas. *Caulerpa racemosa* was not considered in the analysis.

Taxa	Non-invaded areas		Invaded areas	
	A	P	A	P
Encrusting Corallinaceae	56.75	6	0	0
<i>Flabellia petiolata</i> (Turra) Nizamuddin	30.75	6	1.00	3
<i>Padina pavonica</i> (Linnaeus) Thivy	27.25	6	0	0
<i>Halimeda tuna</i> (J. Ellis et Solander) J.V. Lamouroux	17.25	5	0	0
<i>Laurencia obtusa</i> (Hudson) J.V. Lamouroux	15.00	6	0	0
<i>Dictyopteris polypodioides</i> (A.P. De Candolle) J.V. Lamouroux	13.00	6	0	0
<i>Peyssonnelia rubra</i> (Greville) J. Agardh	3.25	5	0	1
<i>Pseudochlorodesmis furcellata</i> (Zanardini) Børgesen	2.25	6	0	0
<i>Jania rubens</i> (Linnaeus) J.V. Lamouroux	1.75	6	0	0
<i>Cladophora prolifera</i> (Roth) Kützing	2.00	4	77.5	6
<i>Hypnea musciformis</i> (Wulfen) Lamouroux	0	0	3.75	6
<i>Ceramium circinatum</i> (Kützing) J. Agardh	0	1	1.25	6
<i>Spyridia filamentosa</i> (Wulfen) Harvey	0	3	1.00	6
<i>Plocamium cartilagineum</i> (Linnaeus) P.S. Dixon	0	3	0.25	6

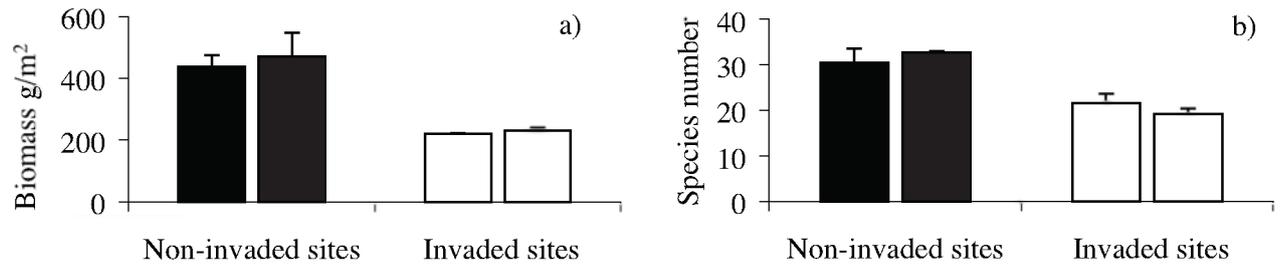


FIG. 1. – Biomass of macroalgae other than *Caulerpa racemosa* and species number of macroalgal assemblages at two non-invaded and two invaded sites (means±SE, n=3).

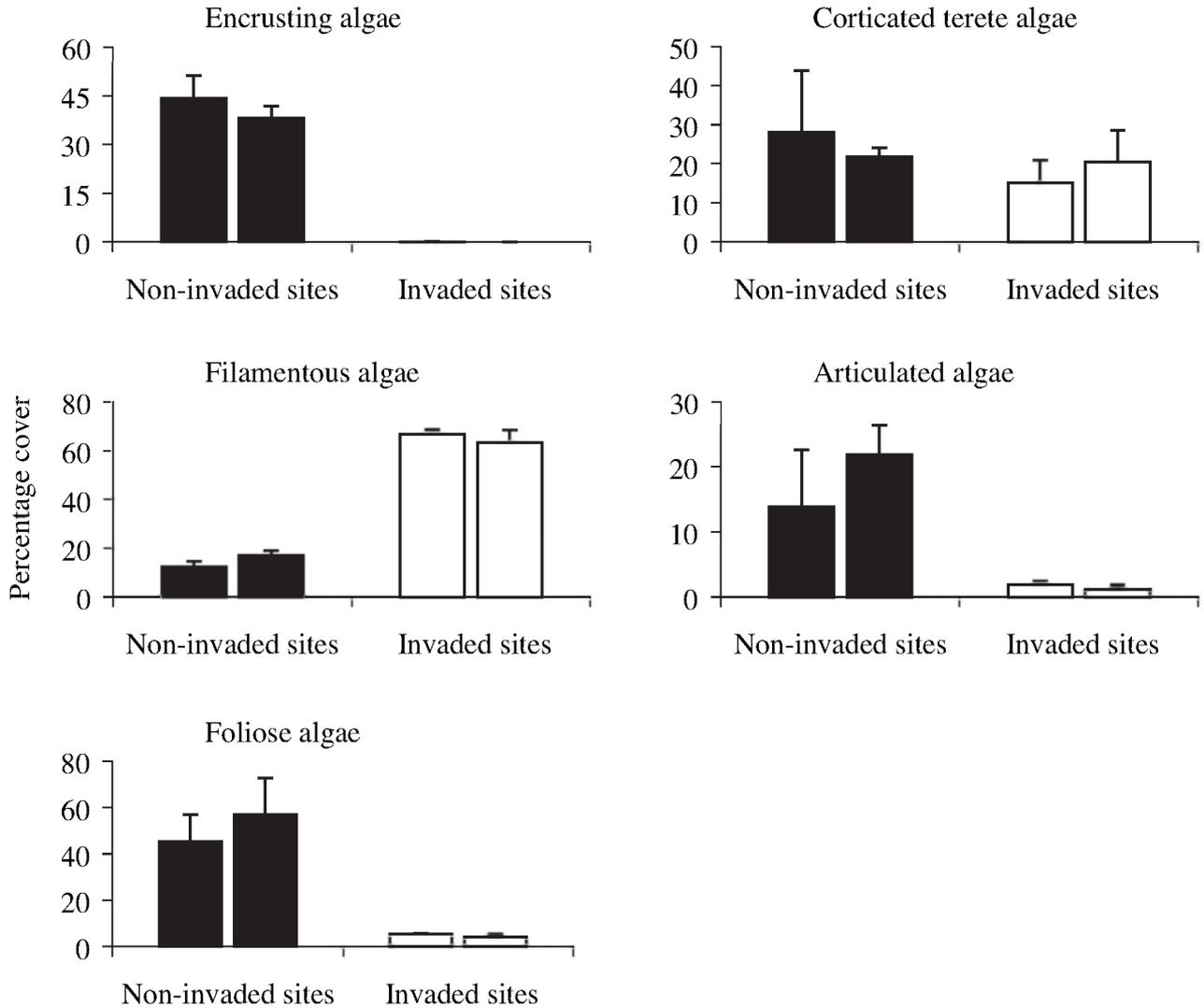


FIG. 2. – Percentage cover of algal morphological groups at two non-invaded and two invaded sites (means±SE, n=3).

number of species was 31.5 ± 1.5 at non-invaded sites and 20.5 ± 1.2 at invaded sites (Fig. 1b). ANOVA detected values significantly higher at non-invaded than at invaded sites for both algal biomass and species number (Table 3). Encrusting, foliose, corticated terete and articulated algae had significantly

higher percentage covers at non-invaded than at invaded sites, while filamentous species were significantly more abundant at invaded than at non-invaded sites (Table 3, Fig. 2). No significant differences were detected in the percent cover of corticated terete species (Table 3). Differences between

TABLE 3. – Results of ANOVA analysis on total biomass, species number and percentage cover of morphological groups. Significant effects are indicated in bold.

Source	df	Biomass		Species number		Encrusting algae		Filamentous algae	
		MS	F	MS	F	MS	F	MS	F
Invasion = (In)	1	1.35	402.80	363.01	44.45	40.33	1912.36	7566.81	282.89
Site (In) = Si(In)	2	0.01	0.12	8.17	0.69	0.02	0.58	26.75	0.93
Residual = Res	8	0.03		11.83		0.04		28.71	
Total	11								
Test C Cochran Trasformation		0.7321 n.s. ln (x+1)		0.7060 n.s. -		0.5679 n.s. ln (x+1)		0.7060 n.s. -	

Source	df	Foliose algae		Corticated terete algae		Articulated algae		Sediment	
		MS	F	MS	F	MS	F	MS	F
Invasion = (In)	1	6463.52	62.40	148.40	2.92	7.48	64.30	40238.18	56.90
Site (In) = Si(In)	2	103.58	0.38	50.85	0.20	0.12	0.25	707.13	0.46
Residual = Res	8	275.44		253.83		0.47		1534.67	
Total	11								
Test C Cochran Trasformation		0.6377 n.s. -		0.7073 n.s. -		0.5713 n.s. ln (x+1)		0.7151 -	

sites were not significant for all variables analysed.

The amount of sediment trapped by algal assemblages was significantly higher at invaded (2962.5±533.4 g m⁻², mean±SE, n=6) than at non-invaded sites (67.1±19.8 g m⁻²) (Fig. 3, Table 3). The ratio between sediment and the total weight of samples (biomass + trapped sediment) showed different values in non-invaded and invaded assemblages: in non-invaded assemblages, the percentage of sediment was very low (13.04±1.74%), while the total weight of invaded assemblages was mostly due to sediment (88.65±1.62%).

Redox potential in the sediment trapped was -189.3 in invaded assemblages and -8.0 in non-invaded assemblages. Sediments were characterised by an

abundant organic carbonate fraction composed mainly of foraminifera, ostracods and fragments of molluscs and echinoids. Inorganic fraction was mainly represented by a mineralogically homogeneous fine-medium sand and scarce well rounded coarse grains. In both the assemblages, sediments were mostly composed of sand (70.63% and 81.59% in non-invaded and invaded assemblages, respectively) and subordinate silt (29.37% and 18.41%). The sediments showed a similar composition, mainly represented by calcite (prevalently of organic origin) and quartz and subordinate albite, orthoclase and clay minerals. The CaCO₃ percentages were 32.48 and 36.76% in non-invaded and invaded assemblages respectively.

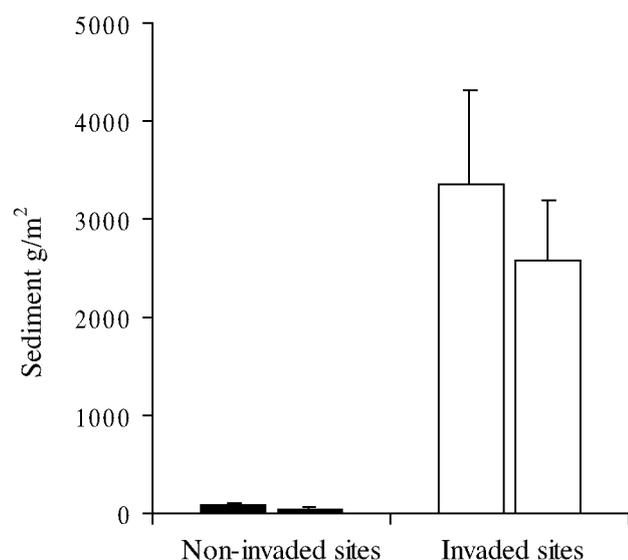


FIG. 3. – The amount of sediment trapped by macroalgal assemblages at two non-invaded and two invaded sites (means±SE, n=3).

DISCUSSION

Assemblages invaded by *Caulerpa racemosa* differed greatly from those that were not invaded. Significant differences were also found in the amount of sediment trapped by the two assemblages.

Differences between invaded and non-invaded assemblages were in agreement with results of previous studies (Piazzi *et al.*, 2001; Balata *et al.*, 2004): encrusting and erect algae, both articulated and foliose, decreased in invaded areas, while opportunistic filamentous species increased their abundance. This result is emphasised by previous studies carried out in the same area before the invasion, which did not show significant differences in the structure of macroalgal assemblages at the same

spatial scales (Piazzi *et al.*, 2001). Macroalgae could be damaged by the overgrowth of the invasive alga, as stolons may stop or extremely reduce the availability of light irradiance. Moreover, species reproducing sexually could be damaged by the lack of substrate available for spore settlement because of pre-emption of substrate by *C. racemosa*.

Both these competition mechanisms could be enhanced by the presence of sediment trapped by stolon mats. The percentage of sediment was 7 times higher at sites invaded by *C. racemosa* than at non-invaded sites. This result suggests the ability of *C. racemosa* to trap and compact sediment. Despite the differences in the amount, characteristics of trapped sediments were similar between invaded and non-invaded sites, suggesting non-selective trapping of sediments by *C. racemosa* mats. The only difference between the two sediments concerned redox values, indicating that below the mats of *C. racemosa* a reduced environment occurs. This finding suggests that effects of *C. racemosa* and sediment can have greater implications on the system. In fact, beside influencing invaded macroalgae, the relevant decrease of redox potential of sediment could also lead to a drastic reduction in diversity of infaunal assemblages (Rosenberg and Nilsson, 2005; Burone *et al.*, 2006).

Sediment constitutes a relevant component in assemblages dominated by *C. racemosa*, suggesting that it could be considered as a structural constituent of *Caulerpa* populations and of algal turfs (Kendrick, 1991; Airoidi and Virgilio, 1998). Trapped sediment could play a role in the competitive mechanisms of *C. racemosa*, based on overgrowth and pre-emption of substrate, in the same way described for mats constituted by introduced turf-forming species (Airoidi, 1998, 2003; Piazzi and Cinelli, 2001).

Results of the present and previous studies allow a synergism between *C. racemosa* and turf-forming algae to be hypothesised. *C. racemosa* colonisation enhances the competitiveness of filamentous species in relation to other algae. Both *C. racemosa* and turfs trap sediments, negatively affecting other algal forms. The seasonal variations in the growth of Mediterranean populations of *C. racemosa* (Ruitton *et al.*, 2005), with peaks of abundance over short periods (Piazzi *et al.*, 2001), could allow the recovery of native algae. However, the modifications in the structure of invaded assemblages lead to a dominance of algal turfs, which continue to accumulate

sediments, making the effects of the invasion more persistent (Piazzi and Ceccherelli, 2006).

Results of this work show that sediment constitutes an important component of *C. racemosa* populations and suggest possible interactions between *C. racemosa*, sedimentation and turfs. Manipulative studies are necessary to verify the model suggested by this descriptive paper and to understand the mechanisms involved.

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