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Co-occurrence of *Caulerpa taxifolia* and *C. racemosa* in the Mediterranean Sea: interspecific interactions and influence on native macroalgal assemblages

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Abstract – The present paper reports the results of two different studies carried out to investigate interactions between naturally mixed Mediterranean populations of *Caulerpa taxifolia* and *C. racemosa* and the effects of their co-presence on native benthic assemblages. Results of the first study showed that co-occurring populations of the two algae exhibited different growth patterns, while growth was similar in single-species patches. *Caulerpa racemosa* did not seem to be affected by the presence of *C. taxifolia*, whereas the latter species stopped growing and decreased in cover in mixed beds. In the second study, macroalgal assemblage showed significant differences in total percent cover and species number between invaded and reference areas. Moreover, total percent cover, diversity and percent cover of filamentous, articulated and crustose algae were lower in *C. racemosa* patches than in *C. taxifolia* patches. In the mixed beds an intermediate situation occurred, with patterns more similar to *C. racemosa* patches. *C. racemosa* seemed to affect macroalgal assemblages more severely than *C. taxifolia* and, in mixed beds, effects of invasion appeared more affected by the presence of *C. racemosa*, though this species colonised more recently the study area.

***Caulerpa racemosa* / *C. taxifolia* / co-occurring / growth / macroalgal assemblages**

Résumé – Présence simultanée de *Caulerpa taxifolia* et de *C. racemosa* en Méditerranée : interactions interspécifiques et influence sur des peuplements algaux naissants. Le présent travail montre les résultats de deux études menées pour évaluer les interactions entre des populations mélangées de *Caulerpa taxifolia* et *C. racemosa* en Méditerranée et les effets de leur présence simultanée sur des communautés benthiques naissantes. Les résultats de la première étude ont montré des accroissements différents entre les populations mélangées des deux algues, alors que le développement était semblable dans les populations isolées. *Caulerpa racemosa* n'est pas apparue influencée par *C. taxifolia*, mais cette dernière a arrêté sa croissance et sa couverture est réduite dans les populations mélangées. Dans la deuxième étude, le peuplement macroalgal a montré des différences significatives pour le pourcentage total de recouvrement et le nombre d'espèces entre les aires envahies et les aires de référence. En outre, le pourcentage total de recouvrement, la diversité et les recouvrements des espèces algales articulées, filamenteuses et encroûtantes ont montré des valeurs plus faibles dans les aires envahies par *C. racemosa* par rapport aux aires envahies par *C. taxifolia*. Dans les aires mélangées il y avait une situation intermédiaire, avec des valeurs plus semblables à celles de *C. racemosa*. *C. racemosa* paraît influencer les peuplements algaux plus profondément que *C. taxifolia* et, dans les populations mélangées, les effets de l'envahissement étaient plus liés à la présence de *C. racemosa*, même si cette dernière espèce a colonisé plus récemment l'aire d'étude.

***Caulerpa racemosa* / *C. taxifolia* / croissance / peuplements de macroalgues / présence simultanée**

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INTRODUCTION

Biological introductions in marine habitats represent a very serious ecological problem (Abrams, 1996; Vitousek *et al.*, 1997) that has been increasing in the last decades, linked to international shipping or aquaculture (Rueness, 1989; Carlton & Geller, 1993; Verlaque & Latala, 1996). Several introduced species show invasive traits, quickly spreading and interfering with native assemblages (Carlton, 1989; Walker & Kendrick, 1998). Many of the most critical invasions are of exotic macroalgae (Carlton & Scanlon, 1985; Critchley *et al.*, 1990; Verlaque, 1994; Ribera & Boudouresque, 1995). The spread and effects of these invasions have been widely studied (Sanderson, 1990; Trowbridge, 1995; Viejo, 1997; Piazzi & Cinelli, 2000), however, little is known about interactions among different invaders and effects on native assemblages caused by the presence of two or more introduced algae. The co-occurrence of several invasive species may, in the future, become a common situation and, in this case, competitive or synergetic mechanisms may establish. The understanding of these mechanisms has to be considered an important goal for ecologists in order to manage invasions, to predict their dynamics and to know their effects on resident communities.

Green algae of the genus *Caulerpa* are considered strong competitors and have been responsible for spectacular invasions in many parts of the world. Invasions are mostly related to introductions (Jousson *et al.*, 2000; Williams & Grosholz, 2002) but in some cases autochthonous populations can become invasive because of changes in biotic or abiotic factors (Davis *et al.*, 1997). In the Mediterranean Sea, the spread of two tropical *Caulerpa* species represents an ecological emergency (Boudouresque *et al.*, 1995; Verlaque *et al.*, 2000).

Caulerpa taxifolia (Vahl) C. Agardh was first identified along the French coasts (Meinesz & Hesse, 1991) and thereafter spread into the western Mediterranean and the Adriatic Sea (Boudouresque *et al.*, 1992; Meinesz *et al.*, 1993; 2001). *Caulerpa racemosa* (Forsskål) J. Agardh was considered a Lessepsian migrant (Lipkin, 1972) and has colonized the eastern part of the Mediterranean Sea since the 1920s (Hamel, 1926) ; in the early 1990s it began to rapidly spread into the western basin (Piazzi *et al.*, 1994; 1997; Gambi & Terlizzi, 1998; Modena *et al.*, 2000), probably as a new introduction (Verlaque *et al.*, 2000).

These two species appear to be highly invasive in the Mediterranean Sea, where they quickly spread through vegetative mechanisms (Ceccherelli & Cinelli, 1999; Smith & Walters, 1999; Ceccherelli & Piazzi, 2001) and appeared strong competitors, resulting in dense populations and possibly affecting biodiversity (Verlaque & Fritayre, 1994; Bellan-Santini *et al.*, 1996; Piazzi *et al.*, 2001b).

The two *Caulerpa* species co-occurred for the first time in the Mediterranean Sea along the coasts of Tuscany, in the northwestern part of the basin (Piazzi *et al.*, 2001a). Growth patterns of the co-occurring populations of the two algae have been compared (Piazzi *et al.*, 2001b) and interspecific competition has been investigated through field transplant experiments (Piazzi & Ceccherelli, 2002). The aims of the present study were to investigate the interactions between naturally mixed populations of *Caulerpa taxifolia* and *C. racemosa* and to evaluate the effects of their co-presence on native benthic communities. To achieve these objectives, two different studies were performed. Growth of the two *Caulerpa* species was evaluated in isolated and mixed patches throughout the period of vegetative growth. To detect differences between macroalgal communities of natural and invaded areas, a combination of multivariate and univariate analyses was used.

MATERIAL AND METHODS

The study site was located along the Tuscany coast (43°28'24" N, 10° 19'42" E) on an exposed rocky platform at 10 m depth. Here, *Caulerpa taxifolia* has been present since 1992 and *C. racemosa* since 1996 (Piazzi *et al*., 2001a). Two studies were carried out to investigate different ecological aspects of the co-presence of the two species.

In the first study, interactions between co-occurring populations of the two species were evaluated. Two areas were randomly chosen in each of the following invaded habitats: patches of *Caulerpa racemosa*, patches of *C. taxifolia* and mixed beds. Three sampling plots of 400 cm^2 were distributed in each area. The corners of each plot were marked with small stakes. Sampling plots were photographed by SCUBA divers in July and October 2001, respectively at the beginning and at the end of vegetative growth period of the two *Caulerpa* species in the Mediterranean Sea (Meinesz *et al*., 1995; Piazzi & Cinelli, 1999). The abundance of the two species was evaluated by projection of slides into a matrix of 100 equally spaced dots: percent cover was assessed by counting the number of dots lying over stolons (Littler & Littler, 1985).

The aim of the second study was to compare the structure of macroalgal assemblages invaded by monospecific or mixed populations of the two *Caulerpa* species. Four different habitats were selected: patches of *C. racemosa*, patches of *C. taxifolia*, patches with the two species mixed between them and zones where *Caulerpa* was not present. Two areas were randomly chosen for each habitat. In October 2001, the peak growth period of the two *Caulerpa* species, two replicated samples were collected in each studied area by removing the biomass from 400 cm^2 surfaces. Material was preserved in 4 % formalin seawater and observed under the microscope to identify macroalgal species and to evaluate cover of each species. Cover was expressed as percentage of sampling surface covered in vertical projection by the species (Boudouresque, 1971). The abundance of *Caulerpa taxifolia* and *C. racemosa* was quantified both as percent cover and biomass of the algae, evaluated as dry weight obtained after 48 h at 60 °C.

For each sample, species number was recorded and total percent cover was calculated. Percent cover of macroalgal morphological groups was also calculated. The following morphological groups were considered: filamentous, foliose, corticated-terete, articulated and crustose (Steneck & Dethier, 1994).

Species number, total percent cover and percent cover of morphological groups were analysed by 2-way ANOVA, with habitat (4 levels) as fixed factor and area (2 levels) as a random factor nested in habitat. Homogeneity of variances was checked by the Cochran C-test and data were ln (x+1) transformed when necessary. A Student Newman Keul's (SNK) test was used for *a posteriori* multiple comparison of means (Underwood, 1997).

Similarity in species composition and abundance between samples was analysed by calculation of Bray-Curtis similarity coefficients. Data were double square root transformed before calculation of Bray-Curtis coefficients. For graphical representation of the data, a two dimensional non-metric multidimensional scaling (nMDS) ordination was carried out. One-way ANOSIM (analysis of similarity) was performed to quantify differences among habitats. Pair-wise differences between the selected habitats were examined through R statistic values, a useful comparative measure of the degree of separation between samples. The separation between habitats was much more significant when all replicates within habitats were more similar to each other than any replicates from different habitats. The

SIMPER (similarity percentage) method was used to evaluate which species were responsible to determine differences between habitats that had been selected in this study (Clarke & Warwick, 1994).

RESULTS

In the control areas, the increase in percent cover between July and October was 16.2 ± 1.5 (means ± SE, n=6) for *Caulerpa racemosa* and 18.0 ± 5.2 for *Caulerpa taxifolia*. In mixed patches, *C. racemosa* cover increased to 13.7 ± 3.2 while *C. taxifolia* cover decreased to 13.0 ± 5.3 (Fig. 1).

In October, the biomass of the two *Caulerpa* species was 1.61 ± 0.18 g dry weight (means ± SE, n=4) for *Caulerpa racemosa* and 4.83 ± 0.91 g for *C. taxifolia* in monospecific beds; in mixed patches the biomass was 1.02 ± 0.39 g and 0.88 ± 0.30 g, respectively.

In the references areas, the most common macroalgae were *Halimeda tuna* (J. Ellis *et* Solander) J.V. Lamouroux, *Flabellia petiolata* (Turra) Nizamddin, *Laurencia obtusa* (Hudson) J.V. Lamouroux and *Cladophora prolifera* (Roth) Kützing. Below them, a turf layer was mostly characterized by *Womersleyella setacea* (Hollenberg) R.E. Norris and *Jania rubens* (Linnaeus) J.V. Lamouroux; encrusting coralline algae covered the substratum.

The total percent cover in the reference areas was 200.2 ± 14.1 (means ± SE, n=4) and the species number was 39.5 ± 0.8. In invaded areas, total percent cover values were 162 ± 33.2 in *C. taxifolia* patches, 64.3 ± 3.0 in *C. racemosa* patches and 75.7 ± 4.9 in mixed patches. ANOVA detected significant differences among habitats for total percent cover and species number, while differences among areas were not significant for the two variables (Tab. 1). The SNK test showed that the two variables were significantly higher in reference sites than in

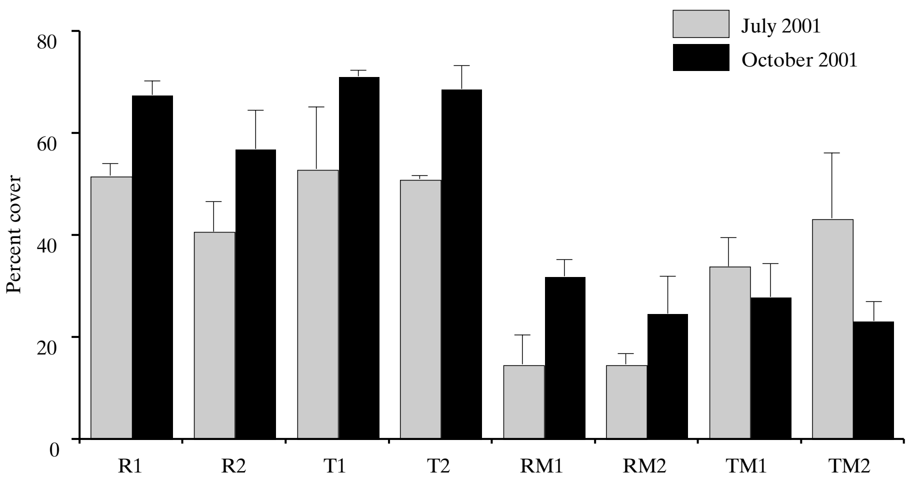

Fig. 1. Percent cover of *Caulerpa taxifolia* and *C. racemosa* in July and October 2001 in isolated (T and R, respectively) and mixed (TM and RM) beds (means ± SE, n=6). Numbers refer to replicated study areas.

Table 1. Results of 2-way ANOVA on total percent cover and species number of macroalgal assemblages. Significant values are written in bold. C = references areas, T = *Caulerpa taxifolia* patches, R = *C. racemosa* patches, M = mixed patches.

		Total percent cover		*Species number*	
Source of variation	*df*	*MS*	*F*	*MS*	*F*
Habitat = H	3	17542.02	**11.13**	208.72	**54.75**
Areas (H)	4	1576.58	1.28	3.81	0.27
Residual	8	1227.10		14.18	
SNK test		C=T>M=R		C>T>M=R	
Cochran's C		0.891		0.744	

invaded areas and species number was higher in *Caulerpa taxifolia* patches (31.5 ± 0.9) than in mixed (25.0 ± 1.1) and *C. racemosa* patches (23.8 ± 0.8).

All morphological groups were well represented in the native macroalgal assemblage. Crustose species were dominant (87.2 ± 1.8 %), but foliose (42.6 ± 12.2 %) and articulated (33.4 ± 11.6 %) algae were also abundant (Fig. 2). ANOVA detected as significant differences between habitats in percent cover of filamentous, crustose and articulated algae, while differences were not significant for foliose and corticated-terete species. SNK test showed that lower values of percent cover of filamentous, crustose and articulated algae were found in *C. racemosa* and mixed patches (Tab. 2).

Non-metric MDS ordination, based on Bray-Curtis similarity coefficients, divided the sites well into distinct groups-reference sites, *Caulerpa taxifolia*, *C. racemosa* and mixed areas (Fig. 3). Results of 1-way ANOSIM examining pair-

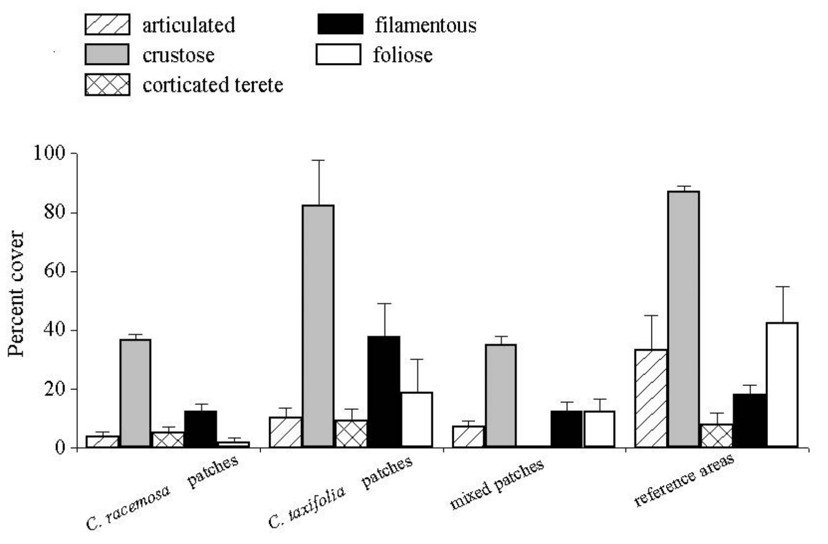

Fig. 2. Percent cover of macroalgal functional groups in reference and invaded areas (means ± SE, n=4).

Table 2. Results of 2-way ANOVA on percent cover of macroalgal functional groups. Significant values are written in bold. C = references areas, T = *Caulerpa taxifolia* patches, R = *C. racemosa* patches, M = mixed patches.

		articulated algae		*crustose algae*		*corticated-terete algae*		*filamentous algae*		*foliose algae*	
Source of variation	*df*	*MS*	*F*	*MS*	*F*	*MS*	*F*	*MS*	*F*	*MS*	*F*
Habitat = H	3	2.16	**136.11**	3191.17	**12.46**	60.22	1.11	0.86	**75.91**	1184.90	3.01
Areas (H)	4	0.01	0.03	256.20	1.07	54.22	2.81	0.01	0.04	393.79	1.59
Residual	8	0.49		238.93		19.31		0.26		247.97	
SNK test		C>T>M>R		C=T>R=M				T>C>R=M			
Cochran's C		0.428		0.859		0.513		0.411		0.460	
Transf.		Ln (x+1)						Ln (x+1)			

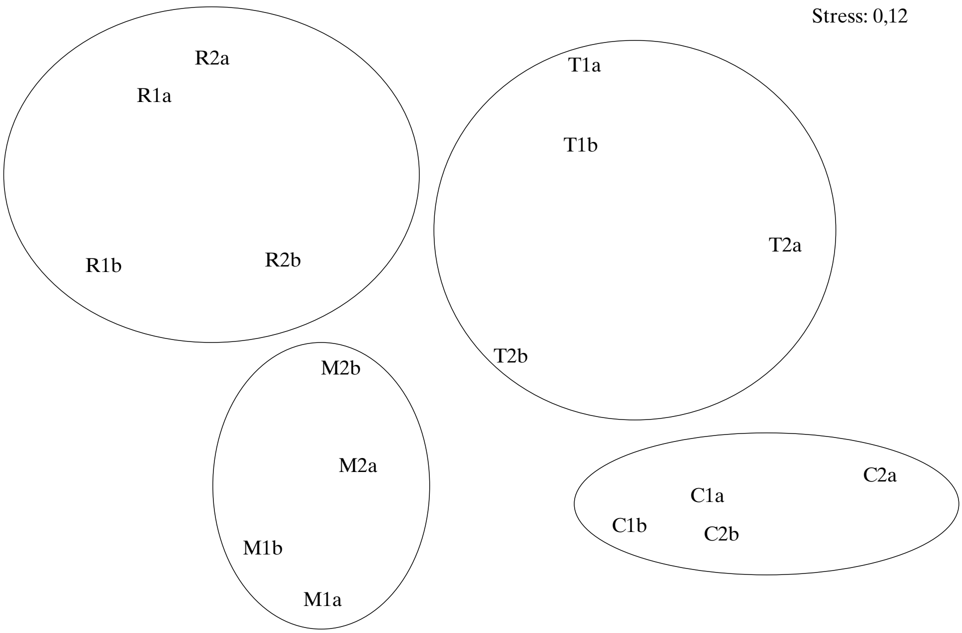

Fig. 3. Non-metric MDS ordination based on Bray-Curtis similarity coefficient applied to species-samples matrix. T = *Caulerpa taxifolia* patches, R = *C. racemosa* patches, M = mixed patches, C = reference areas. Numbers refer to study areas and letters to replicates.

wise differences between groups are shown in Tab. 3. The high values of R indicate that there were differences in assemblage composition at the selected habitats: in particular *C. racemosa* and mixed patches were strongly separated from reference and *C. taxifolia* patches. The SIMPER test showed that *Flabellia petiolata* was the principal species that contributed to separate reference sites from

Table 3. Global R values of 1-way ANOSIM test examining pair-wise differences between habitats. The number of permutations is 35.

	Global R
C. racemosa patches vs. *C. taxifolia* patches	0.99
C. racemosa patches vs. references areas	1
C. racemosa patches vs. mixed patches	0.729
C. taxifolia patches vs. references areas	0.75
C. taxifolia patches vs. mixed patches	0.78
reference areas vs. mixed patches	0.94

Table 4. Results of SIMPER test on percentage contributions of taxa to determine significant differences between habitats.

	Encrusting coralline	*Flabellia petiolata*	*Halimeda tuna*	*Womersleyella setacea*
C. racemosa patches vs. *C. taxifolia* patches	33.6 %	9.7 %	–	22.8 %
C. racemosa patches vs. references areas	29.3 %	24.6 %	–	–
C. racemosa patches vs. mixed patches	9.3 %	14.3 %	–	11.3 %
C. taxifolia patches vs. references areas	–	23.1 %	19.3 %	14.1 %
C. taxifolia patches vs. mixed patches	34.8 %	10.2 %	–	19.5 %
reference areas vs. mixed patches	32.2 %	22.2 %	–	–

invaded areas, while encrusting coralline and *Womersleyella setacea* mostly separated reference sites and *C. taxifolia* patches from *C. racemosa* and mixed patches (Tab. 4).

DISCUSSION AND CONCLUSIONS

Results of the present study showed that naturally co-occurring populations of *C. taxifolia* and *C. racemosa* exhibited different growth patterns, while growth was similar in single-species patches. *Caulerpa racemosa* did not seem to be affected by the presence of *C. taxifolia*. In contrast, the latter species' cover decreased in mixed beds. *Caulerpa taxifolia* was present in the study area before *C. racemosa* and this latter species started to invade established *C. taxifolia* patches at the beginning of the 2001 warm season. *Caulerpa racemosa* seemed to affect *C. taxifolia* from the first phases of colonization. The lack of a formal BACI design does not allow attribution of the effect of *C. racemosa* in decreasing *C. taxifolia* cover in mixed plots, as other factors may be involved. However, the results of the present study are in agreement with those of manipulative transplant experiments (Piazzi & Ceccherelli, 2002) and differences in *C. taxifolia* growth between isolated and mixed patches were so evident that it seems reasonable to suppose *C. racemosa* represented the main factor determining the observed patterns.

Interspecific interactions between the two species are not clear. Members of the Caulerpales are strong competitors that may interfere with other species through several mechanisms. The stoloniferous structure of *Caulerpa* allows them to easily overgrow other benthic organisms, sometimes causing their elimination (Verlaque & Fritayre, 1994; Davis *et al.,* 1997). Moreover, competition may occur by production of allelochemical substances (Lemée *et al.*, 1993; Ricci *et al*., 1999) and exploitation of resources by rhizoid uptake of nutrients (Chisolm *et al*., 1996). Mechanisms that regulate interactions between these two invaders have not been investigated and therefore all the above-mentioned mechanisms could be involved. However, direct interactions through allelochemical substances seem to be the most likely mechanism involved because of the early development of effects. Moreover, Aliya & Shameel (1998) detected differences in fatty acids, sterols and diterpenes among *Caulerpa* species, suggesting peculiarities in chemical composition within the genus.

Macroalgal assemblages showed significant differences between invaded and reference areas, in agreement with those described in other Mediterranean studies (Verlaque & Fritayre, 1994; Piazzi *et al*., 2001b). Macroalgal assemblages in *C. racemosa* patches were more different from reference sites than those in *C. taxifolia* patches. In particular, encrusting coralline algae and *Womersleyella setacea* strongly decreased in areas invaded by *C. racemosa*. These results confirm the different effects of the colonization by the two species already observed in previous separate studies (Verlaque & Fritayre, 1994; Piazzi *et al*., 2001b). In mixed beds, an intermediate situation occurred, with patterns more similar to *C. racemosa* patches.

In the studied area, *C. racemosa* seemed to affect macroalgal assemblages more strongly than *C. taxifolia*. In mixed beds, the overall effects of *Caulerpa* invasion appeared to be more influenced by the presence of *C. racemosa*, despite this species having colonised more recently.

This study confirms previous observations on the high invasive ability of *Caulerpa racemosa* (Piazzi *et al*., 2001a; Piazzi & Ceccherelli, 2002). However, a longer period of investigation is necessary to study the evolution of mixed beds, and further experimental studies are needed to clarify the effects of the co-presence of the two *Caulerpa* species and to examine the mechanisms involved in their interactions.

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