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Different Effects of *Caulerpa racemosa* on Two Co-occurring Seagrasses in the Mediterranean

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In this study, we present the results of a 14-month field experiment on the effects of the introduced alga *Caulerpa racemosa* on two co-occurring native seagrasses, *Cymodocea nodosa* and *Zostera noltii*. The experiment was conducted in a mixed shallow seagrass bed along the Tuscan coast (Italy) that has been invaded by the alga since 1995. Treatment consisted of the manipulation of the presence of the alga (presence vs. removal). Response variables considered for *Cymodocea nodosa* were shoot and flower (both male and female) density and for *Zostera noltii* were vegetative and reproductive shoot density, the first species being dioecious and the latter monoecious. Results have indicated that the presence of the alga influences shoot density of both plants. With *Cymodocea nodosa* the shoot density was lowered and with *Zostera noltii* it was increased in areas invaded by the alga. Both *Cymodocea nodosa* flower density and *Zostera noltii* reproductive shoot density were found to be significantly higher where *Caulerpa racemosa* was present relative to where it was removed. Hence, different effects, either positive or negative, of the alga were found depending on the species and response variable. Potential mechanisms of interaction are discussed.

Introduction

Non-indigenous species can seriously affect the integrity of natural communities by both their remarkable invasion and their possibility to change community structure and ecosystem function through the extinction or reduction of native species (Bertness 1984, Nichols *et al.* 1990, Trowbridge 1995, Grosholz and Ruiz 1995, Abrams 1996, Ceccherelli and Cinelli 1997, Reusch and Williams 1998, Ruiz *et al.* 1999, Byers 2000, Grosholz *et al.* 2000). In this regard, a fundamental goal for ecologists is to understand how invading species influence established communities and native species, which offers potentially a critical test of the relative importance of interspecific competition, predation and species equilibrium in the structuring of natural communities.

Displacement of existing flora by introduced algal species, intentionally or accidentally, has been widely reported (Critchley *et al.* 1990, Hay 1990, Sanderson 1990, Sindermann 1991, Chambers *et al.* 1993). Mediterranean macroalgal assemblages have been shown to be vulnerable to seaweed invasions as indicated by Verlaque and Fritayre (1994) for the invading *Caulerpa taxifolia* (Vahl) C. Agardh and by Piazzi *et al.* (2001) for *Caulerpa racemosa* (Forsskål) J. Agardh. For *C. racemosa,* descriptive data have suggested that it greatly alters native macroalgal assemblages affecting primary turf and encrusting species relative to erect species (Piazzi *et al.* 2001). Also, non-indigenous seaweeds have been claimed to reduce the distribution of native seagrasses by competitively displacing them (Druehl 1973, Norton 1976, Ceccherelli and Cinelli 1997). In the context of the loss of seagrass habitat, biological invaders have in fact been regarded as a great threat. For example, *Sargassum muticum* (Yendo) Fensholt settles in *Zostera marina* L. beds and has been claimed to interfere with its regeneration, since no seagrass germlings were found where the alga was present (Den Hartog 1997). In the Mediterranean Sea, the successful invasive alga *Caulerpa taxifolia* is also claimed to be a cause of the loss of *Posidonia oceanica* (L.) Delile (Meinesz and Hesse 1991, Boudouresque *et al.* 1992, Meinesz *et al.* 1993), which displays lower shoot density and yellowish leaves where invaded (Villèle and Verlaque 1995). In contrast, however, near the town of Menton, seagrass distribution has remained similar despite the invasion of the alga (Jaubert *et al.* 1999). Furthermore, experimental evidence of the impact on resident species has rarely been accomplished (but see Ceccherelli and Cinelli 1997), particularly for the interactions between introduced *Caulerpa* and the seagrasses.

The rhizophytic *Caulerpa racemosa* is a green alga (Bryopsidales) widely distributed in tropical seas and it has been spreading in the Mediterranean Sea since it was first recorded (Hamel 1926). Quite recently it has reached the north-western part of the basin (Piazzi *et al.* 1997a, 1997b, Piazzi and Cinelli 1999) where it exhibits the typical features of a successful invading species, given its high abundance in most of the habitats of occurrence (Piazzi *et al.* 2001). Here, *C. racemosa* has great competitive ability to overgrow non-erect species and thus affect turf and encrusting species (Piazzi *et al.* 2001). In *Posidonia oceanica* and *Cymodocea nodosa* (Ucria) Ascherson habitats this alga overgrows the rhizomes of the seagrasses (Ceccherelli *et al.* 2000); therefore, species interaction in these systems may occur both in the below and above ground compartments, interfering respectively with nutrient acquisition and light availability.

At the study site *Caulerpa racemosa* has invaded a mixed seagrass bed composed of *Cymodocea nodosa* and *Zostera noltii* Hornem.; both seagrasses are relatively small, fast-growing colonising species which commonly co-occur in mixed meadows in the central and north-western Mediterranean Sea. The aim of this work was to study the modifications caused by the presence of *Caulerpa racemosa* on both seagrass species by the experimental removal of the alga.

Materials and Methods

This study was carried out from December 1997 until February 1999 at Antignano (Livorno, Italy), on the Tuscany coast (43°28'24"N and 10°19'42"E). At this site the mixed shallow seagrass bed composed of *Cymodocea nodosa* and *Zostera noltii* has been invaded by the introduced alga *Caulerpa racemosa* at least since 1995, when it was found for the first time. Within this site we have randomly chosen 4 areas (about 6 m^2 in size) and, in each of them, eight permanent plots (40 x 40 cm) were randomly positioned. The treatment consisted of the removal of *Caulerpa racemosa* from two areas, while the other two were left undisturbed as controls. Removal treatment was accomplished manually during biweekly visits to the site.

Response variables considered were shoot and flower (both male and female) density of *Cymodocea nodosa* and vegetative and reproductive shoot density of *Zostera noltii*, the first being dioecious and the latter monoecious. In the field, at each sampling time, a subreplicate square (10 x 10 cm) was placed in the centre of each permanent plot and seagrass shoots were counted, while density of reproductive structures was estimated by counting flowers and reproductive shoots in the whole permanent plot (40 x 40 cm). During the study period, data of vegetative shoot density were taken on 7 occasions (December 1997, March, May, July, October and November 1998, February 1999), whereas the reproductive structures were sampled once, on 1 June 1998.

To analyse data, two-way ANOVAs were performed for all variables. For the vegetative shoot density of both species, data analysed were those relative to the last sampling time (February 1999). Removal 'treatment' was treated as a fixed factor while 'area' as random and nested in the 'treatment'. Cochran's test was used prior to ANOVA to test the assumption of variance homogeneity.

Results

Cymodocea nodosa shoot density underwent great temporal fluctuations where *Caulerpa racemosa* was not present (Fig. 1A) showing low mean values during winter (1800 shoot/m^2), increasing during spring and reaching maximum values in July (3800 shoot/m^2). Conversely, *Cymodocea nodosa* dynamics were greatly altered by the presence of the alga: shoot density was very low during spring, moderately increased in summer and reached the maximum value in July (1800 shoot/m^2), then decreased again during autumn (Fig. 1B). Hence, overall seagrass shoot density was higher where the alga was removed. However, ANOVA performed on the last sampling date has not shown significant differences between treatments, highlighting that the presence of *C. racemosa* had no effect on the seagrass density in winter. A significant difference was observed between areas indicating that the plant growth depends on area characteristics since plant response is spatially heterogeneous (Table I).

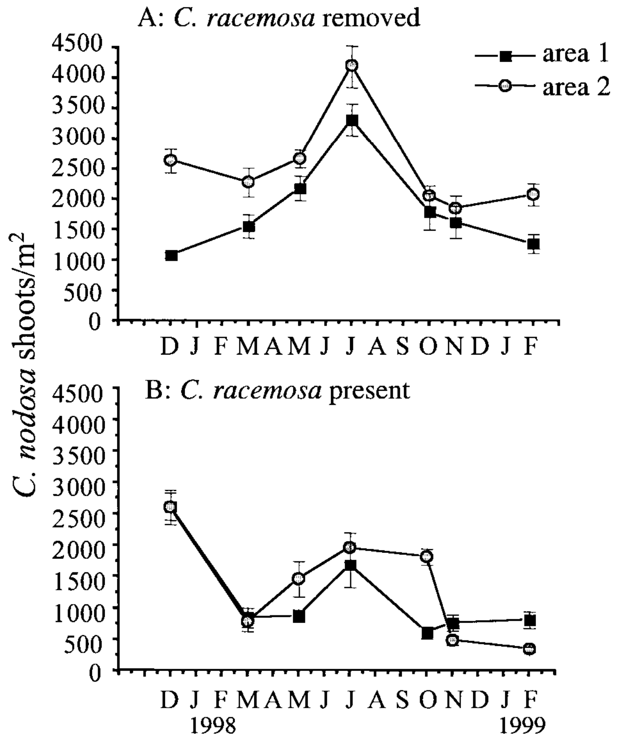

Fig. 1. Temporal variation of *Cymodocea nodosa* mean (±SE) shoot density (A) in *Caulerpa racemosa* removal treatment and (B) in controls. Data relative to each experimental area are shown (n = 8).

Opposite results were found for *Zostera noltii*. Great temporal fluctuations were found where *Caulerpa racemosa* was present, with very low values at the start of the study (about 400 shoot/m^2, in December 1998) that increased during spring and remained high during summer until the end of the study (Fig. 2B). Conversely, in the removal treatment, density did not fluctuate and remained low for the whole period, always inferior to 1000 shoot/m^2 (Fig. 2A). Analyses using ANOVA on the last sampling data showed significant differences between treatments, indicating that the presence of *C. racemosa* affects the seagrass density (Table I). Conversely to *Zostera noltii*, *Cym-*

Table I. Results of multifactorial analysis of variance on shoot density of *Cymodocea nodosa* and *Zostera noltii* on the last sampling date (February 1999).

Source of variation	df	*Cymodocea nodosa*		*Zostera noltii*	
		F	*P*	*F*	*P*
C. racemosa = CR	1	5.49	0.1438	1881.74	**0.0005**
Area (CR) = A	2	11.44	**0.0002**	0.05	0.9493
Error	28				
Cochran's test $C_{critic} = 0.52$		C = 0.43		C = 0.52	

CR = *C. racemosa* (presence vs. absence); A = Area (2 areas). Bold type indicates significance ($p < 0.05$).

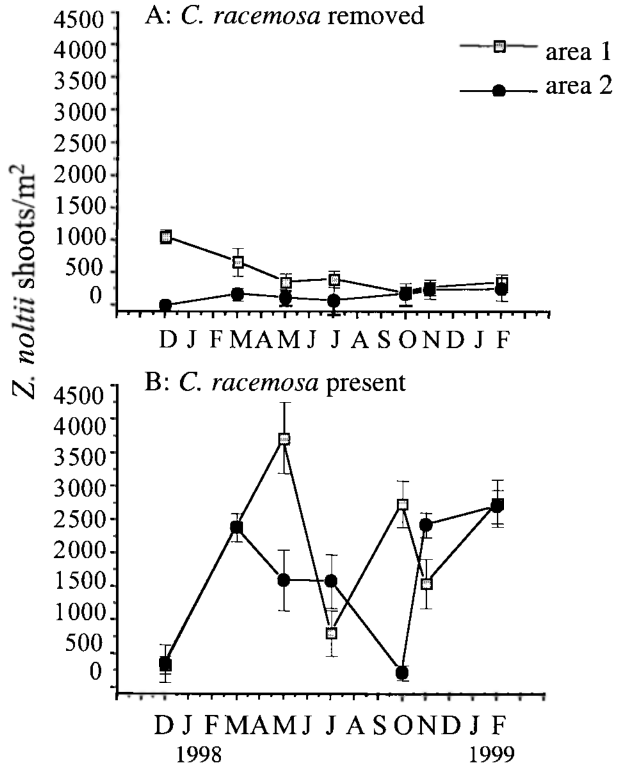

Fig. 2. Temporal variation of *Zostera noltii* mean (± SE) shoot density (A) in *Caulerpa racemosa* removal treatment and (B) in controls. Data relative to each experimental area are shown (n = 8).

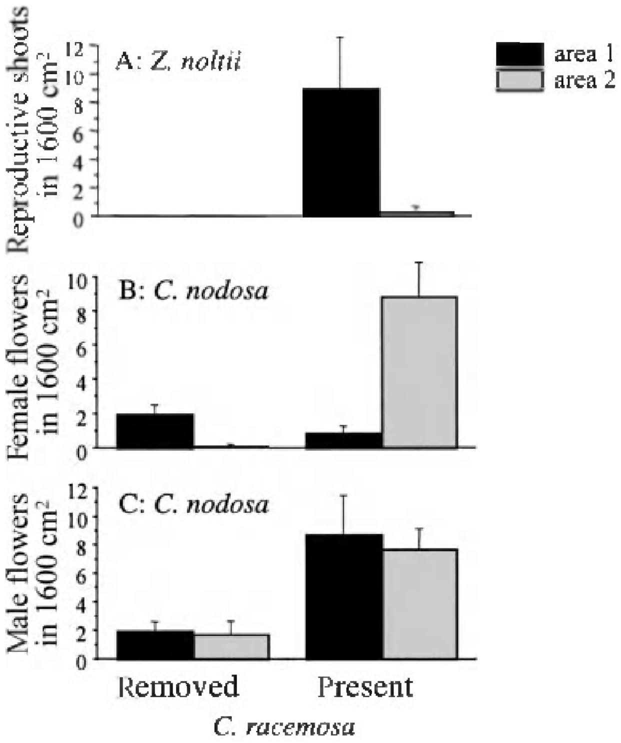

Fig. 3. Mean (± SE) density of reproductive shoots of *Zostera noltii* (A) and of female (B) and male (C) flowers of *Cymodocea nodosa* in *Caulerpa racemosa* removal treatment and in controls. Data relative to each experimental area are shown (n = 8).

odocea nodosa shoot density was homogeneous among areas (Table I).

Zostera noltii reproductive shoots occurred only in areas where the alga was present, although a great difference was found between these two areas (Fig. 3A). Unfortunately, analysis of variance was not performed on this response variable because variance heterogeneity could not be removed even after transformation. A significant influence of the presence of *Caulerpa racemosa* was found on flower density of *Cymodocea nodosa.* Male flowers of the seagrass were more frequent where the alga was present (Fig. 3B) while female flowers were almost significantly affected (p = 0.0561, Table II and Fig. 3C). Male flowers were homogeneously distributed among areas while female flowers had a heterogeneous spatial distribution (Table II).

Discussion

Our findings suggest a contrasting influence of *Caulerpa racemosa* on seagrass shoot density, being positive on *Zostera noltii* and negative on *Cymodocea nodosa.* Enhancement of reproductive structures of

Table II. Results of multifactorial analysis of variance on flower density of *Cymodocea nodosa* (male and female) and reproductive shoot density of *Zostera noltii* in June 1998.

Source of variation	df	*Cymodocea nodosa*			
		male flower		female flower	
		F	*P*	*F*	*P*
C. racemosa = CR	1	111.04	**0.0089**	17.57	**0.0561**
Area (CR) = A	2	0.20	0.8169	27.34	**0.0000**
Error	28				
Transformation		Log(x + 1)		Log(x + 1)	
Cochran's test		C = 0.36		C = 0.32	
$C_{critic} = 0.52$					

CR = *C. racemosa* (presence vs. absence*)*; A = Area (2 areas). Bold type indicates significance ($p < 0.05$). Cochran's test for *Zostera noltii* reproductive shoot density was significant even after transformation and analysis had not been performed.

both seagrasses was found where the alga was present.

An interesting feature worth noting is that, when *Caulerpa racemosa* was removed, *Cymodocea nodosa* shoot density fluctuated consistently with season as described for this species by other authors (Terrados and Ros 1992, Pérez and Romero 1994, Reyes *et al.* 1995, Rismondo *et al.* 1997, Kraemer and Mazzella 1999). Conversely, *Zostera noltii* dynamics were not in accordance with the results obtained for this species by other studies. Indeed, when *Caulerpa racemosa* was removed, seagrass shoot density did not vary through time and remained very low during the whole study, while temporal fluctuations have been commonly indicated (Van Lent *et al.* 1991, Vermaat and Verhagen 1996, Cebrián *et al.* 1997, Kraemer and Mazzella 1999). These findings suggest that at this site local characteristics, either abiotic or biotic, regulate plant dynamics.

The results obtained for flowers and reproductive shoots suggest that the presence of *Caulerpa racemosa* is a stimulating factor for sexual reproduction for both *Cymodocea nodosa* and *Zostera noltii*. In general, many authors have suggested that sexual reproduction occurs in seagrasses more frequently in areas slightly colonised or in conditions of environmental stress (Phillips *et al.* 1983, Curiel *et al.* 1996). Moderate burial, for example, has been shown to increase the allocation of resources to sexual reproduction (Marbà and Duarte 1994, 1995). The expansion of *Caulerpa racemosa* on *Cymodocea nodosa* might represent a facilitating condition for reproduction because it enhances burial: in fact, the stratified growth of stolons of the alga is likely to make a trapping system for deposition of sediment (personal observation) that, at this site, constitutes a relevant phenomenon (Airoldi *et al.* 1996).

Studies based on nitrogen acquisition, storage and use by the two co-occurring seagrasses indicate that, in sites characterised by anthropogenic input of excess nutrients and reduced water column transparency, *Zostera noltii* may, over time, replace *Cymodocea nodosa* (Kraemer and Mazzella 1999). In fact, when the competition is for light the favour is predicted to go towards the species with greater potential for photosynthetic production (*Zostera noltii*) relative to maintenance costs (*Cymodocea nodosa*) (Kraemer and Mazzella 1999). In this study, the areas where *Caulerpa racemosa* occurs are likely to be more sediment-influenced than alga-free ones (personal observation) and here, thus, seagrass competition for light might be more intense. We believe that the alga may indirectly affect, through burial, the interaction between the two seagrasses (interaction modifications), thus influencing the abundance of both species (Wootton 1993). A multifactorial approach which includes manipulation of siltation and density of both seagrasses is needed to evaluate this hypothesis. However, this study can only generate hypotheses and is not devoted to identification of potential mechanisms through which *Caulerpa racemosa* affects the two seagrasses. Rather, as a starting point, we intended to assess the nature of the effects of the introduced alga on the two seagrasses as a function of its presence.

This study suggests that the presence of the alga simultaneously enhances and depresses seagrass populations depending on species and response variable and this result has been rarely accomplished (but see Reusch 1998).

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