

Threat to macroalgal diversity: effects of the introduced green alga *Caulerpa racemosa* in the Mediterranean

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ABSTRACT: *Caulerpa racemosa* is a tropical green alga introduced into the Mediterranean probably as an immigrant from the Red Sea. This study evaluated the modifications caused by *C. racemosa* invasion on the structure of the benthic macroalgal community near Leghorn (northwestern Mediterranean). To achieve this objective, we studied invasion by *C. racemosa* of algal assemblages on 2 different substrata by monitoring the structure of the phytobenthic community before and after the invasion of the alga and comparing our results with assemblages not invaded by *C. racemosa*. Results showed that the invasive alga *Caulerpa racemosa* completely covered the surface of both types of substratum 6 mo after the start of the invasion. With rapid horizontal elongation of the stolons (up to 2 cm d⁻¹) *C. racemosa* overgrew native macroalgal species within 4 mo. As a consequence, phytobenthic community structure deeply changed: species cover, number and diversity greatly decreased. Furthermore, the relative importance among vegetation layers of the macroalgal assemblage changed: turf and encrusting species were deeply affected while erect species survived after 1 yr of the invasion. During the period from December to May, when both cover and biomass of *C. racemosa* diminished, the macroalgal community did not return to initial conditions. Instead, the structural changes increased in the following season, indicating the importance of *C. racemosa* invasion on a local scale.

KEY WORDS: *Caulerpa racemosa* · Introduced species · Invasion · Macroalgae · Species diversity

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INTRODUCTION

Biological invasions affect the integrity of natural communities in many different ecosystems (Vitousek et al. 1997). This adverse process is increasing, especially in the marine environment where it is linked to the intensification of international shipping, aquaculture and aquarium activity (Carlton 1989, Carlton & Geller 1993, Verlaque 1994, Ribera & Boudouresque 1995). However, in comparison to an extensive literature documenting the rate of spread and current distribution of non-indigenous species (Carlton & Scanlon 1985, Piazzì et al. 1994, Russell & Balazs 1994, Cohen

et al. 1995, Piazzì et al. 1997), quantitative studies on the effects of marine invasions on resident communities are rare (but see Bertness 1984, Trowbridge 1995, Grosholz & Ruiz 1995, Abrams 1996, Ceccherelli & Cinelli 1997, Reusch & Williams 1998). In this regard, a further fundamental goal for ecologists is to estimate the vulnerability of different communities to invasions (Burke & Grime 1996, Rejmánek & Richardson 1996, Thébaud et al. 1996, Williamson & Fitter 1996, Dukes & Mooney 1999, Ceccherelli et al. 2000). Structural modifications of native communities may depend on the characteristics of both invaded systems and of introduced species (Stachowicz et al. 1999).

Displacement of existing flora by introduced algal species, intentional or accidental, has been widely reported (Sindermann 1991, Chambers et al. 1993),

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mostly in relation to large Phaeophyta, as *Undaria pinnatifida* (Harvey) Suringer (Hay 1990, Sanderson 1990) and *Sargassum muticum* (Yendo) Fensholt (Critchley et al. 1990). Replacement of dominant macroalgae by introduced species may result in changes of the species composition and their trophic food webs.

In the Mediterranean Sea, more than 60 macroalgal species were introduced up until 1995 (Ribera & Boudouresque 1995). Many of these species have not only established themselves, but have become invasive, influencing abundance of autochthonous species. Their spread is likely to deeply change the structure of native benthic communities, affecting biodiversity of the ecosystems. This phenomenon has occurred, for example, in the western Mediterranean as consequence of the invasion of the Chlorophyta *Caulerpa taxifolia* (Vahl) C. Agardh (Meinesz & Hesse 1991) and of 2 Rhodophyta, *Acrothamnion preissii* (Sonder) Wollaston (Piazzi et al. 1996) and *Womersleyella setacea* (Hollenberg) R.E. Norris (Airoldi et al. 1995).

Caulerpa racemosa (Forsskål) J. Agardh is a green alga (Bryopsidales) widely distributed in tropical seas. Since the beginning of this century it has been colonising the eastern Mediterranean (Hamel 1926), and based on the chronology of records (e.g. Aleem 1948, Lipkin 1972) it is inferred to be a Lessepsian immigrant. Only recently has it spread into the north-western part of the basin (Piazzi et al. 1994) quickly invading infralittoral areas along Italian and French coasts (Bussotti et al. 1996, Piazzi et al. 1997, Gambi & Terlizzi 1998, Verlaque et al. 2000) where it rapidly expanded its distribution invading all kind of substrata between 0 and 40 m depth (Piazzi et al. 1997, De Biasi et al. 1999). Taxonomical, ecological and biogeographical data suggest that 3 distinct taxa of *C. racemosa* coexist in the Mediterranean and that the invasive variety, which has quickly spread since the early 1990s throughout most of the Basin, appears closest to the *C. racemosa* var. *occidentalis* (Verlaque et al. 2000).

Preliminary observations have suggested that *Caulerpa racemosa* replaces native algae in invaded areas (Piazzi pers. obs.). Although in the Mediterranean Sea this alga is considered invasive, the effects of its presence on benthic ecosystems have not been investigated yet. The aim of this work was to study the modifications caused by *C. racemosa* invasion on the structure of the benthic macroalgal community, either on matte and rock substratum, with the attempt to evaluate species and conditions more vulnerable to the invasion of the alga. To achieve this objective, the algal assemblages occurring on 2 different substrata were monitored before and after the invasion of the alga. Structural variables of the phytobenthic community were also analysed.

MATERIAL AND METHODS

The study site is a subtidal area in 2 m depth, located near Leghorn along the Tuscan coast (43° 30' N, 10° 20' E), where *Caulerpa racemosa* has been found since 1995 either on rocky bottom and dead matte of the marine phanerogam *Posidonia oceanica* (L.) Delile (Piazzi & Cinelli 1999). At this site the rocky bottom is covered by algal assemblages and by patches of *P. oceanica*; also zones of dead matte of this seagrass occur. *P. oceanica* matte is formed by the growth of rhizomes and roots of the seagrass and by the accumulation of sediment, which make up quite high matte structures; if there are no more seagrass shoots, it is called dead matte (Molinier & Picard 1952).

For the experiment, 4 areas (2 on *Posidonia oceanica* dead matte and 2 on rocks) were randomly chosen during spring 1998. Each area was rectangular (3 × 10 m) about 30 m². In each area, 2 zones were chosen: one next to a *Caulerpa racemosa* meadow so that during the study period it would have been invaded by the alga (invaded), and the other one not close to *C. racemosa* (control). For each zone, 2 replicates were taken on each sampling date so that a total of 12 replicates were randomly taken for the whole study. Each replicate consisted, in the total surface scraping, of 400 cm². Replicates were at least 40 cm away from each other and, in the invaded zones, the same distance from the advancing edge. Six sampling times were chosen for this study: in the invaded zones the start of invasion by *C. racemosa* occurred in July 1998, with samplings done in May 1998 before the algal invasion, and then in August 1998, October 1998, April 1999 and October 1999.

Samples were preserved in 4 % solution of formaldehyde in seawater and observed under microscope to determine macroalgal species and to estimate cover of each species. Cover was expressed as a percentage of surface covered in vertical projection by the species (Boudouresque 1971).

For each sample, species number (N) was recorded and total percent cover (R) and Shannon-Weaver diversity index (H') were calculated. Percent cover of the 3 vegetation layers (turf layer, encrusting and erect layer) was also calculated (Verlaque & Fritayre 1994, Airoldi et al. 1995). The abundance of *Caulerpa racemosa* was quantified both as cover and biomass of the alga, evaluated as dry weight obtained after 48 h at 60°C.

Each of these response variables were analysed using 4-way ANOVAs with *Caulerpa racemosa* presence (vs absence) and substratum type (matte and rock) treated as fixed factors and area (2 levels) and time (5 levels) as random. Area was considered nested in the substratum while all other factors were orthogonal. Cochran's test was used prior to the analyses and SNK test to compare levels of significant factors.

RESULTS

Caulerpa racemosa rapidly invaded the experimental surfaces, as shown by dynamics in cover and biomass (Fig. 1). In August 1998, only 3 mo after the start of the invasion, *C. racemosa* percent cover reached values of $83.8 \pm 1.6\%$ (mean \pm SE) on rocky bottom and $81.1 \pm 2.8\%$ on dead matte. In November 1998 both substrata were completely covered (Fig. 1A). The abundance fluctuated with time, decreasing during spring 1999 to $19.1 \pm 3.7\%$ on rocky bottom and $23.9 \pm 2.8\%$ on dead matte, and reaching 100% at the end of October 1999 on both types of bottom (Fig. 1A). Patterns between substrata were very similar.

Caulerpa racemosa biomass followed similar temporal fluctuations, reaching 237.5 ± 18.5 g dw m^{-2} on rocks and 447 ± 67.5 g dw m^{-2} on dead matte in October 1998. Biomass diminished in spring 1999, while in October 1999 it was similar to the previous year (Fig. 1B). At the end of the study period, a significant greater biomass was found on matte compared with the rock substratum (ANOVA, $F_{1,4} = 53.61$, $p = 0.0181$).

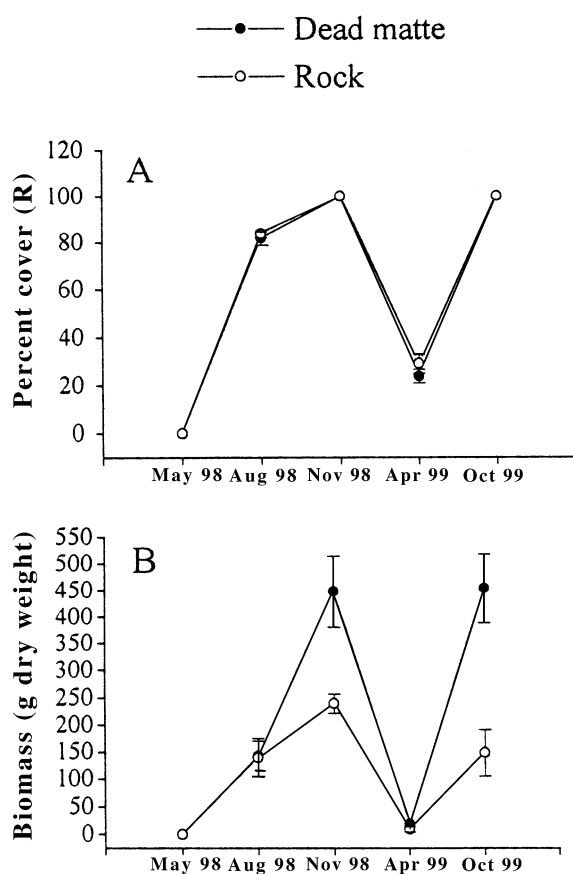


Fig. 1. Temporal variation in mean (\pm SE) *Caulerpa racemosa*. (A) Percent cover and (B) biomass on dead matte of *Posidonia oceanica* and rocky bottom ($n = 4$)

In the macroalgal assemblage at the study site, 94 species were identified on *Posidonia oceanica* dead matte and on rocky bottom. Among them 14 Chlorophyta, 69 Rhodophyta and 11 Fucophyceae species were recorded and each assigned to a vegetation layer (Table 1). The erect layer was dominated on rocky bottom by *Halopitys incurvus*, *Halopteris scoparia*, *Cladophora prolifera* and *Halimeda tuna*, while on dead matte by *Flabellia petiolata*, *C. prolifera* and *H. scoparia*. In spring the Dictyotales *Dictyota dichotoma* and *Padina pavonica* were also important. The turf species—mainly consisted in filamentous species, such as *Dasya rigidula*, *Womersleyella setacea*, *Acrothamnion preissii*, *Falkenbergia rufulanosa*, *Spyridia filamentosa* and *Herposiphonia secunda*—also occurred as epiphyte on erect algae. The encrusting layer was present only on rocky bottom and was characterized by encrusting Corallinaceae and *Peyssonnelia* spp. Among all macroalgal species found at the site, 10 were endemic to the Mediterranean (Table 1).

In May 98, before *Caulerpa racemosa* invasion, species number was 39.2 ± 1.5 (hereafter mean \pm SE, $n = 8$) and 37 ± 1.5 on rocky bottom and on dead matte, respectively (Fig. 2A,B), while macroalgal cover was, respectively, 134.1 ± 3.3 and 126.3 ± 8.1 (Fig. 2C,D). On the same sampling date, macroalgae species diversity (H') was 2.16 ± 0.13 on rocky bottom and 2.01 ± 0.09 on dead matte (Fig. 2E,F). After invasion of *C. racemosa*, species number, percent cover and diversity of macroalgae decreased progressively (Fig. 2). Analysis of variance performed on species number (Table 2) detected a significant effect of the presence of the alga depending on time: a higher number of species was found in the pre-invasion time where *C. racemosa* was absent, compared to where it was present. Furthermore, although species number was very heterogeneous among areas with time, it also depended on substratum type ($p = 0.0036$), being higher on rocky bottoms. A higher number of macroalgal species was found after the invasion where *C. racemosa* was absent, relative to where it was present (Fig. 2A,B). The analysis on macroalgal species diversity (H') was done only on data obtained on the last sampling date (October 99) because of heteroscedasticity of all the data (Table 3). The presence of the introduced alga also influenced macroalgae percent cover, as values were much lower in the invaded areas than in the controls (Fig. 2C,D). Unfortunately, differences in macroalgal species cover between zones invaded by *C. racemosa* and controls could not be detected because of variance heterogeneity ($C = 0.397$ for untransformed data, $C_{critic} = 0.0237$), even after transformation. The presence of *C. racemosa* as well as the type of substratum significantly affected species diversity, although their influence was not mutually dependent

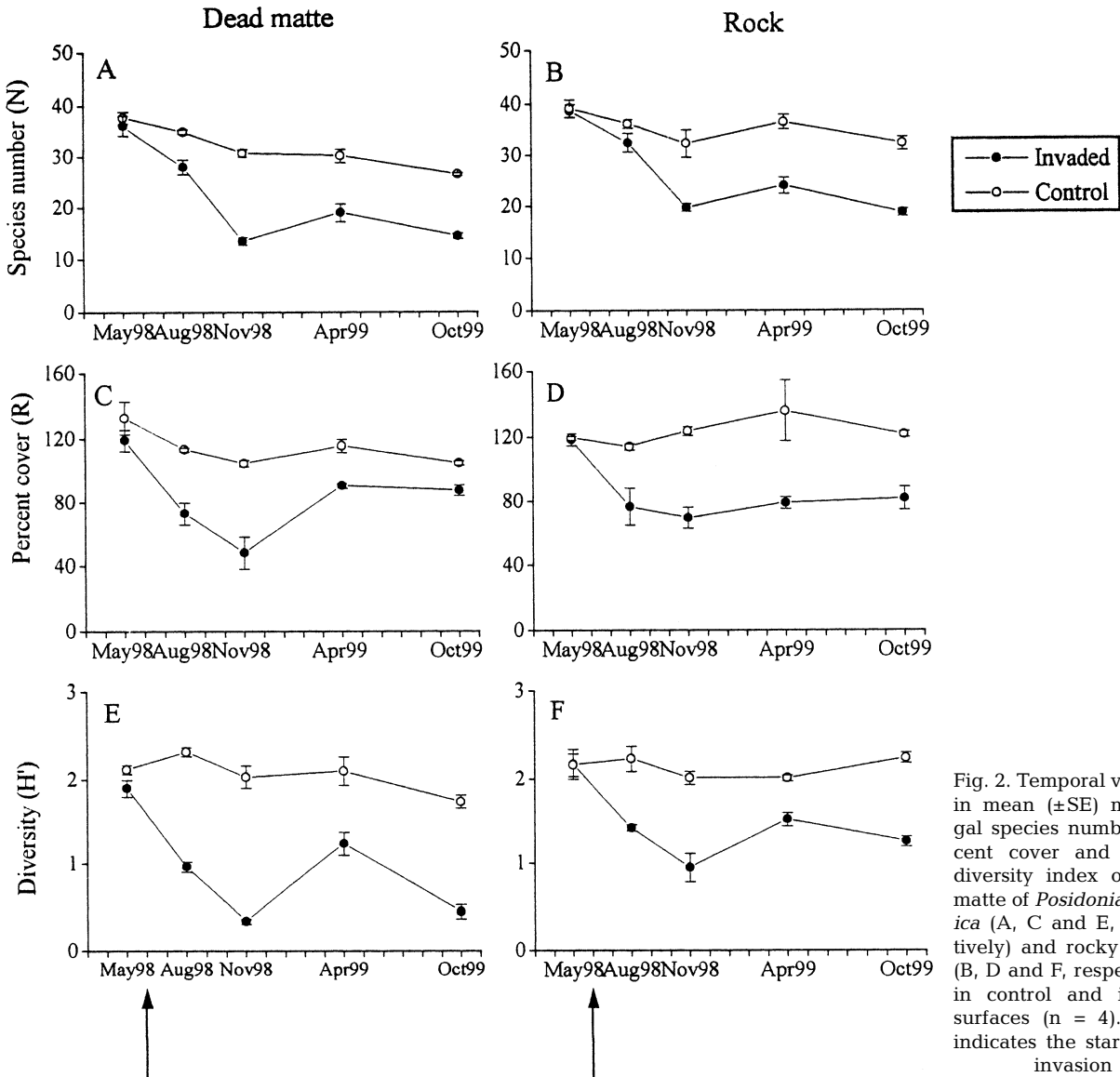


Fig. 2. Temporal variation in mean (\pm SE) macroalgal species number, percent cover and species diversity index on dead matte of *Posidonia oceanica* (A, C and E, respectively) and rocky bottom (B, D and F, respectively) in control and invaded surfaces (n = 4). Arrow indicates the start of the invasion

(interaction not significant). H' was found to be higher where the alga was not present in both types of substratum (Fig. 2E,F).

The invasion of *Caulerpa racemosa* affected the 3 vegetation layers of macroalgal community differently (Fig. 3). Percent cover of turf species on matte substratum was significantly affected by the presence of the alga while, on rocky bottom, there were no significant differences in percent cover of turf species between areas invaded by *C. racemosa* and those not invaded (Table 4, Fig. 3A,B). Overall, where the alga was not present, a greater percent cover of turf species was found on matte substratum than on rocky bottom at all sampling times after the invasion of the alga, while values relative to May 1998 (pre-invasion time) were very

similar between substrata. Conversely, where the alga was present, abundance of turf species on matte substratum was found to be not significantly different than on rocky bottoms at all sampling times. In October 1999, at the end of the study, after 15 mo of invasion, turf species cover was $152.5 \pm 37.5 \text{ m}^2$ and $415 \pm 55 \text{ m}^2$ on matte and rocky substratum, respectively.

Encrusting macroalgal percent cover was very different between substrata, being almost lacking on dead matte of *Posidonia oceanica*. The presence of *Caulerpa racemosa* had a significant effect on this response variable only on rocky bottom, being higher only after invasion where the alga was not present (Table 4). After August 1998 where the alga was present, encrusting species cover on the 2 substrata was

Table 2. Analysis of variance on the number of species; Cochran's test was not significant ($C = 0.230$, $C_{critic} = 0.237$). C = *C. racemosa* (presence vs absence); S = Substrate (matte vs rocks); A = Area (2 areas); T = Time (5 sampling dates). Bold type indicates significance ($p < 0.05$). SNK tests are not shown because the particular ordering of levels identified would add nothing to results of the *F*-test

Source of variation	df	MS	F	p
C	1	1814.51		
S	1	357.01	37.16	0.0036
A(S)	2	7.81		
T	4	617.60		
C × S	1	1.51	0.44	0.5276
C × A(S)	2	1.56	0.45	0.6525
C × T	4	148.54	42.82	0.0000
S × T	4	9.60	0.46	0.7621
A(S) × T	8	20.78	2.66	0.0193
C × S × T	4	4.04	1.16	0.3939
C × A(S) × T	8	3.46	0.44	0.8871
Error	40	7.81		

similar, while, in alga-free areas, abundance was higher on rocks. At the end of the study where the alga was present, cover by these species reached 12.5 ± 5 m² on rocks while it was completely lacking on matte (Fig. 3C,D).

Cover of erect macroalgae was significantly affected by *Caulerpa racemosa*, progressively with time (Fig. 3E,F) and differently on the substrata. At the end of the experiment where the alga was absent, erect macroalgae cover was greater on rock than on matte, while their abundance was greater on matte in the areas with *C. racemosa* (Table 4). The analysis detected that a significant proportion of the variance could be due to an

Table 3. Analysis of variance on species diversity (H') on the last sampling date; Cochran's test was not significant ($C = 0.417$, $C_{critic} = 0.680$). C = *C. racemosa* (presence vs absence); S = Substrate (matte vs rocks); A = Area (2 areas). Bold type indicates significance ($p < 0.05$). SNK tests are not shown because the particular ordering of levels identified would add nothing to results of the *F*-test

Source of variation	df	MS	F	p
C	1	51529.0	214.82	0.0000
S	1	17030.2	70.99	0.0000
A(S)	2	385.6	1.61	0.2590
C × S	1	992.2	4.13	0.0764
C × A(S)	2	407.1	1.69	0.2429
Error	8	239.9		

effect of the specific location of the area. Great fluctuations in cover of erect species were detected as a function of time on matte (Table 4), being lower on autumn sampling dates relative to the spring ones (Fig. 3E,F). On rocky bottom, no significant effect of time was detected.

Thus, among macroalgal layers, the encrusting species were relatively more affected by *Caulerpa racemosa*, while the erect species survived after 1 yr of invasion. However, at the study area all dominant erect species were also present at the end of the study period on both substrata, except for *Halopitys incurvus* that, on dead matte, was not present after the first 2 sampling dates (Table 1). Conversely, the dominant encrusting species were strongly affected, since after August 1998 *Peyssonnelia bornetii* and *P. rubra* were not found on matte, and *P. bornetii*, *P. stoechas* and encrusting Corallinaceae on rock. The dominant turf

Table 4. Results of multifactorial analysis of variance on encrusting, turf and erect species percent cover: C = *C. racemosa* (presence vs absence); S = Substrate (matte vs rocks); A = Area (2 areas); T = Time (5 sampling dates). Bold type indicates significance ($p < 0.05$). SNK tests are not shown because the particular ordering of levels identified would add nothing to results of the *F*-test

Source of variation	df	Encrusting		Turf		Erect	
		F	p	F	p	F	p
C	1						
S	1						
A(S)	2	0.32	0.7329	0.388	0.6904		
T	4						
C × S	1						
C × A(S)	2	0.94	0.4293	1.000	0.2430	5.570	0.0305
C × T	4						
S × T	4						
A(S) × T	8	0.20	0.9888	1.360	0.2430	0.565	0.8001
C × S × T	4	35.05	0.0000	7.298	0.0089	9.812	0.0035
C × A(S) × T	8	0.90	0.5252	0.537	0.8216	0.217	0.9859
Error	40						
Cochran's test		$C = 0.296$		$C = 0.184$		$C = 0.220$	
$C_{critic} = 0.237$							

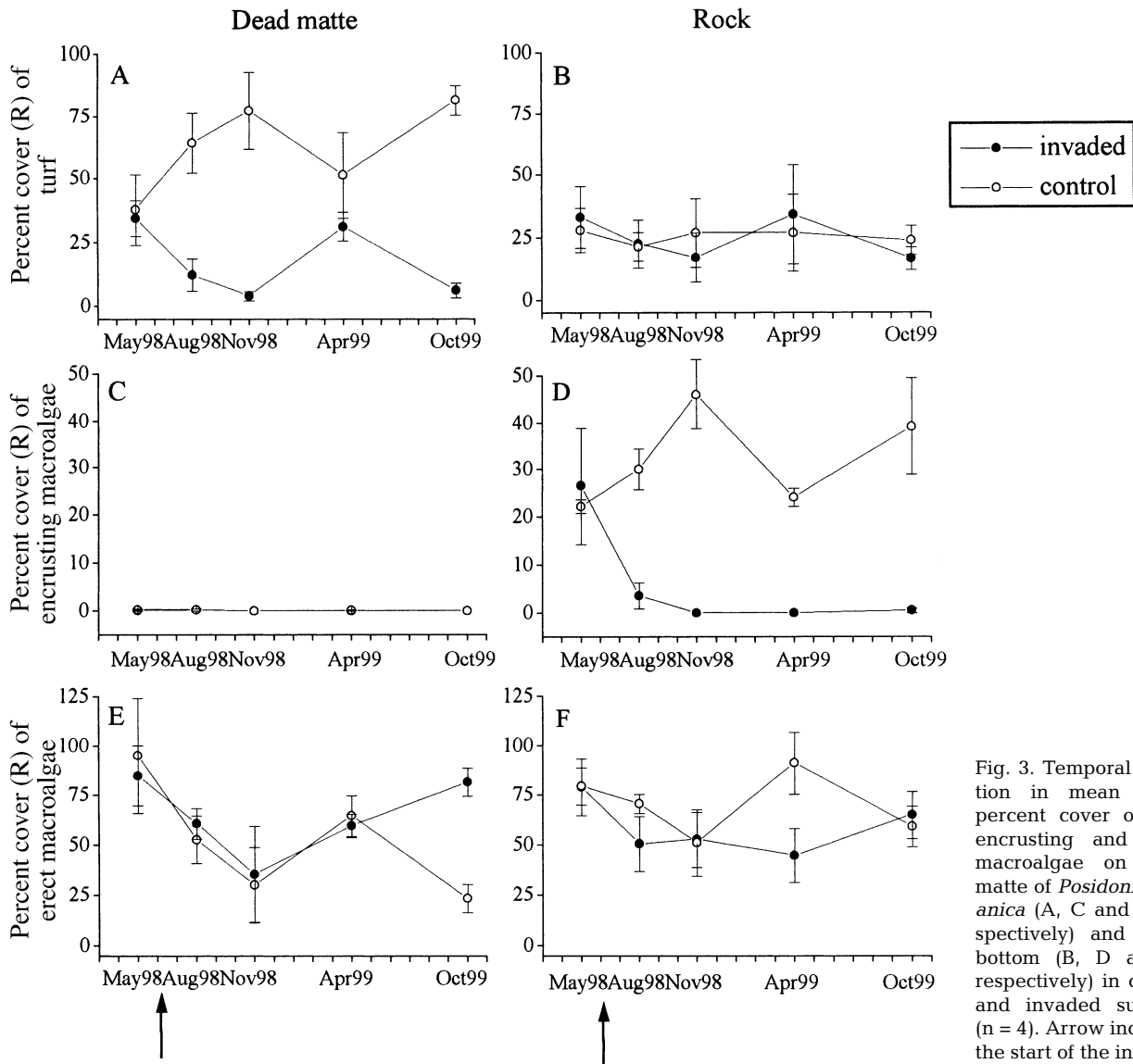


Fig. 3. Temporal variation in mean (\pm SE) percent cover of turf, encrusting and erect macroalgae on dead matte of *Posidonia oceanica* (A, C and E, respectively) and rocky bottom (B, D and F, respectively) in control and invaded surfaces ($n = 4$). Arrow indicates the start of the invasion

species *Acrothamnion preissii*, *Womersleyella setacea* and *Spyridia filamentosa* persisted all through the study period. Particularly Cladophorales appeared the most resistant to the invasion.

Among the endemic species found the most vulnerable to the invasion of *Caulerpa racemosa* were *Aglaothamnion tenuissimum*, *Feldmannophycus raysiae* and *Peyssonnelia bornetii*. In fact, they were abundant in the first sampling dates but greatly decreased during *C. racemosa* invasion. At the end of the study, they had disappeared in the experimental units invaded. Conversely, other species such as *Bryopsis cupressina* and *Acrodiscus vidovichii* were present, even if sporadically, both before and during invasion of the alga, being independent of the presence of *C. racemosa*.

DISCUSSION

Results of this experimental work stresses the great invasive ability and the strong competitive characteristics of the introduced alga *Caulerpa racemosa* (see also Piazzini et al. 1997, Piazzini & Cinelli 1999, Ceccherelli et al. 2000). *C. racemosa* rapidly invaded both rock substratum and dead matte of *Posidonia oceanica* where macroalgal assemblages were present and it had completely covered the surface of both types of substrata after 6 mo from the start of the invasion. Conversely, there was more biomass of *C. racemosa* found on matte than on rocks, suggesting a more favourable condition of the former type of substratum for the overgrowth of the alga. In fact, the fast horizontal elongation of the stolons (growth reached 2 cm d^{-1}) allowed

the alga to easily overgrow the other macroalgal species (Piazzi et al. 1999). After stolons completely occupied all available substratum, continuing vertical growth of the thallus formed a multilayer structure of *C. racemosa*. A subsequent trapping of sediment damages native species.

At the study site the macroalgal assemblage showed a high species diversity: species composition was similar to that described for other shallow assemblages of the same zone (Cinelli 1969, Airoldi et al. 1993, Piazzi et al. 1999). The macroalgal community was impoverished by *Caulerpa racemosa* invasion. Species cover, number and diversity of macroalgae fell, and the relative abundance among vegetation layers greatly changed. Encrusting species were more affected compared to erect species, which survived after 1 yr of invasion.

The decrease in species diversity has already been shown in benthic ecosystems as a result of invasions of alien species (Verlaque & Fritayre 1994, Airoldi et al. 1995, Piazzi et al. 1996, Walker & Kendrick 1998). Sensitivity of native algae to different invaders varies. For example, susceptibility of specific species identified in this study was different in comparison with that described for algal assemblages colonised by *Caulerpa taxifolia* in the Mediterranean (Verlaque & Fritayre 1994). As a result of *C. taxifolia* colonisation, fleshy algae with their epiphytes disappeared before filamentous species, while encrusting species showed the highest resistance (Verlaque & Fritayre 1994). These effects on the native community could be due to different competitive behaviours of the 2 introduced species. *C. taxifolia*, having a quite tall canopy, can easily compete with erect species compared to *C. racemosa* that has small blade size (a few centimetres); however, the former is unable to cover the substratum quickly while the latter can totally cover the substratum in a very short time.

In this study, *Caulerpa racemosa* abundance followed the same temporal fluctuations described for other Mediterranean *Caulerpa* spp. (Meinesz 1979, Meinesz et al. 1995, Komatsu et al. 1997, Ceccherelli & Cinelli 1998): a period of vegetative growth between June and November alternated with a period of vegetative rest from December to May. During this period, despite the fall of cover and biomass, some stolons remained on the bottom, allowing for a fast total invasion of the substratum at the beginning of the following summer. Obviously, the period of vegetative rest of *C. racemosa* did not allow the macroalgal community to restore the native structure since modifications had persisted in the assemblage and had increased in the following season. This trend suggests the strong decrease in species diversity of the areas invaded by the alga.

Overall, the higher species number and diversity index found for the macroalgal assemblage on rocks, relative to that on dead matte, suggests a higher vulnerability to invasion of *Caulerpa racemosa* for the assemblage present on the latter substratum (Stachowicz et al. 1999). On the other hand, this result could be also due to the different biomass of *C. racemosa* present on the 2 types of substratum, hence to the greater capability of the alga to invade macroalgal community on dead matte of *Posidonia oceanica* than on rocks.

The capability of the introduced alga to grow and invade different substrata can be influenced by the presence of particular species, as already inferred by Ceccherelli et al. (2000). Both the re-establishment of drifting fragments of thallus and the growth of established colonies of *Caulerpa racemosa* are likely to be influenced by other species through both direct and indirect mechanisms. For example, turf algae can mechanically catch drifting fragments of the alga and, by trapping sediment, they can enhance nutrient availability of the substratum. Further experimental studies are needed to address questions about the nature of the interaction between the introduced alga and the native species, and to elucidate the mechanisms responsible for the interaction.

In general, communities are said to be invulnerable when an introduced species is able to establish and persist or expand (Burke & Grime 1996). As suggested by Crawley (1987), Rejmànek (1989) and Reusch & Williams (1999) a dense cover of established indigenous species can be a major factor reducing the probability of successful invasion. The results of this study suggest that the macroalgal community on both dead matte and rocks can be said to be invulnerable. Furthermore, the well established indigenous macroalgal assemblage, occurring at the study site on both substrata, although dense in cover, became invaded by the introduced alga in a relatively short time.

If resistance of native species to invasion means being invaded but not displaced, the Mediterranean native macroalgal assemblages cannot be said to be resistant to the invasion of *Caulerpa racemosa*. Conversely, *Posidonia oceanica* meadows that have been invaded by the alga for some years are not affected in terms of density, suggesting a great resistance to invasion (Piazzi pers. obs.). However, all these Mediterranean communities, macroalgae on rocky substratum, macroalgae on dead matte of *P. oceanica* (this study) and *P. oceanica* meadows (Ceccherelli et al. 2000) are invulnerable by the alga. Resistance to displacement is likely to be dependent on density of the indigenous species cover, as suggested by Crawley (1987) and Rejmànek (1989), and on plants' capability to buffer against environmental variability, but also on species canopy size which confers different competitive ability.

Seagrass and erect macroalgae canopy height are important attributes regulating species resistance to the invasion of *C. racemosa*, attributes that turf and encrusting species do not possess. However, the role of canopy height of native plants on the effect of the alga invasion has still to be experimentally investigated.

This work represents a first attempt to evaluate and characterise modification of native macroalgal Mediterranean assemblages due to *Caulerpa racemosa* and how different strata of the indigenous algae are affected. However, further studies are necessary to observe long-term effects on the macroalgal benthic community and to know whether the difference between substrata effect of *C. racemosa* on macroalgal species number and diversity, observed in this study, persists.

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