

Effects of competition between two introduced *Caulerpa*

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ABSTRACT: Competitive interactions between 2 introduced algae, *Caulerpa taxifolia* and *C. racemosa*, were studied in 2 experiments. The first separately evaluated the interspecific and intraspecific effects on both species by manipulating their abundance. The second investigated the fate of fragments of *C. taxifolia* transplanted into patches of *C. racemosa*, in contrast to those established on algal turfs. *C. racemosa* and *C. taxifolia* had similar temporal trends in growth but reached different sizes. The overall increase in stolon length at higher densities for both species suggested that positive interactions are very important. However, there was a significant interspecific effect on *C. taxifolia* stolon length but no effect on *C. racemosa*. Furthermore, *C. taxifolia* fragments transplanted into *C. racemosa* patches showed clear signs of stress with respect to those transplanted into algal turfs: blades became blanched and eroded. Overall, the results of this study suggest that growth increases with density augmentation, therefore suggesting that invasive characteristics of the species may increase with the time of colonisation. Both species tend to spread faster at higher density. Overall, where both species co-occur, we predict that *C. racemosa* would be the favoured species as regards the outcome of competition.

KEY WORDS: *Caulerpa taxifolia* · *Caulerpa racemosa* · Competition · Introduced species · Positive interaction

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INTRODUCTION

Biological introductions in marine ecosystems are widely reported and over the last years they have shown an increasing trend linked to the development of international shipping, aquaculture and aquarium activity (Carlton 1989, Carlton & Geller 1993, Verlaque 1994, Ribera & Boudouresque 1995). In many cases, introduced species are able not only to establish themselves but they also tend to become invasive, affecting native ecosystems (Grosholz & Ruiz 1995, Trowbridge 1995, Abrams 1996, Reusch & Williams 1998). The lack of natural enemies, predators or competitors, makes introduced species potential invaders. The success of invasive species is generally linked to their growth,

reproduction and dispersal strategies together with the ability of populations to persist. In many cases, introduced species have the potential to radically alter the structure and function of native ecosystems causing a decrease of biodiversity (Vitousek 1990, Airoldi et al. 1995, Grosholz & Ruiz 1995, Ceccherelli & Cinelli 1997, Walker & Kendrick 1998, Piazzi & Cinelli 2000). When 2 or more introduced species co-occur, competitive interaction between them or synergetic deleterious effects on indigenous species could occur. One of the important goals for ecologists is to understand interactions among invasive species in order to predict possible effects on colonised communities.

Biological invasions by macroalgae are widely reported in many benthic systems (Critchley et al. 1990, Hay 1990, Sanderson 1990, Sindermann 1991, Chambers et al. 1993, Russel & Balazs 1994, Verlaque 1994, Ribera & Boudouresque 1995). In the Western Medi-

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terranean Sea, the successful introduction of the *Caulerpa* species is particularly worrying. In 1984, *C. taxifolia* (Vahl) C. Agardh was recorded in the Mediterranean along Monegasque coasts (Meinesz & Hesse 1991) and since then it has quickly colonised wide areas of the Mediterranean (Boudouresque et al. 1992, 1994, Meinesz et al. 1993, 1998). *C. racemosa* (Forskål) J. Agardh is considered an immigrant from the Red Sea and has been spreading for a long time in the Southeastern Mediterranean (Hamel 1926, Aleem 1948, Lipkin 1972) and recently in the Western Mediterranean (Piazzi et al. 1994, 1997, Bussotti et al. 1996, Gambi & Terlizzi 1998, Verlaque et al. 2000).

Both species showed high invasive characteristics and caused deep modifications of benthic communities, mostly related to the decreasing species diversity (Verlaque & Fritayre 1994, Bellan-Santini et al. 1996, Piazzi et al. 2001). Interactions between the 2 introduced species and the native flora have been experimentally investigated (Ceccherelli & Cinelli 1997, 1999a, Ceccherelli et al. 2000). Competitive ability of the 2 congener species could be similar if this was based on plant traits (Olson & Lubchenco 1990). Both species have stolons which are able to quickly elongate, easily overgrow other macroalgal species (Meinesz et al. 1995, Piazzi et al. 1997) and have a high potential of dispersal by fragmentation and re-establishment of stolons (Ceccherelli & Cinelli 1998, Ceccherelli & Piazzi 2001).

The 2 introduced species first co-occurred in the Mediterranean in a restricted area along the Tuscan coast (Piazzi et al. 1999) and, more recently, along the French coast (A. Meinesz pers. comm.). The interactions between these 2 congener algae offer a unique opportunity to investigate the competitive outcome between 2 species that have similar life strategies, growth, reproduction and physiological adaptations. This knowledge would offer an important insight into the effects of this interaction on their colonisation rate.

The aim of this work is to investigate competitive interactions between *Caulerpa taxifolia* and *C. racemosa*, simultaneously studying the effect of inter- and intraspecific competition. This has been done by separately evaluating the effect of intra- and interspecific increases in density on each of the species, and their interrelationship. To achieve these objectives, 2 reciprocal experiments (competition experiments) were performed through manipulation of the abundance of the species.

This work also aims to investigate the fate of fragments of *Caulerpa taxifolia* when they establish in patches of *C. racemosa* in contrast to when they establish on algal turfs. Fragments of *C. taxifolia* can easily re-establish after they are uprooted (Ceccherelli & Cinelli 1999a). The *C. taxifolia* transplant experiment,

which consists of experimental transplants of *C. taxifolia* in both habitats, reproduces a natural situation occurring at the site, where dense mats of *C. racemosa* have colonised wide surfaces, while *C. taxifolia* is distributed in smaller patches.

MATERIAL AND METHODS

Study site. The study site is located south of Leghorn (43° 28' 24" N and 10° 19' 42" E) on an exposed shore at a depth of 10 m. The bottom is characterised by a rocky platform colonised by a photophilous turf-dominated macroalgal assemblage, composed mainly of *Womersleyella setacea* Hollenberg (Airoldi et al. 1995) and patches of the marine seagrass *Posidonia oceanica* (L.) Delile. The study was carried out from July 1998 to September 1999.

Competition experiments. The first experiment tested the effect of intra- and interspecific competition on *Caulerpa taxifolia* and *C. racemosa*, respectively. In each experiment, transplant material consisted of fragments of *C. racemosa* and *C. taxifolia* bearing the stolon (10 cm long), rhizoids and blades. Each experimental unit consisted of a 20 × 20 cm surface in which fragments were anchored using plastic covered metal staples (Ceccherelli et al. 2000). Transplants were done on a *Posidonia oceanica* dead 'mat' because it is a suitable substrate that guarantees a high success of transplantation (Ceccherelli & Cinelli 1999b, Piazzi et al. 2001). Unfortunately extended areas at the site of *Posidonia oceanica* dead 'mat' were not frequent because *C. racemosa* had already naturally colonised many of the available areas. Furthermore, transplanting *C. taxifolia* fragments far from this site would not have been ethical because, unlike *C. racemosa*, this alga is not present in other areas in Tuscany. The poor replication used in the present experiments was thus influenced by the limited availability of substrata suitable for transplants at the site.

The controls consisted of a chosen density (2 fragments) of 1 species which was then compared to experimental plots with different fragment density (2 + 2 and 2 + 4 fragments) of each species alone or in combination. Hence, each experiment consisted of the following 5 treatments (Table 1): (1) 2 fragments of Species A (controls), (2) 4 fragments of Species A, (3) 6 fragments of Species A, (4) 2 fragments of Species A and 2 fragments of Species B, and (5) 2 fragments of Species A and 4 fragments of Species B. In the first experiment, Species A was *Caulerpa taxifolia* and Species B was *C. racemosa*, while in the second experiment species were oppositely assigned. The comparison among Treatments 1, 2 and 3 detects intraspecific interactions in each species while detection of inter-

specific competition was evidenced by the comparison of Treatments 1, 4 and 5 (Underwood 1986, 1992, 1997). Treatments were interspersed and there were 3 replicates for each treatment spaced at about 5 m apart. The whole experimental area was about 250 m².

Transplanting was undertaken in July 1998, because previous studies showed that summer is the best season to ensure transplant success of either *Caulerpa taxifolia* or *C. racemosa* (sensu Chapman 1986). Fragments of the alga, complete in portions, were manually uprooted from areas of the same depth and fixed to the substratum of experimental units within 1 h using 2 plastic covered metal U-shaped hooks per fragment that stapled the stolon to the substrata. All fragments were taken from the same area and we assumed that possible effects of differing initial sizes of blades and rhizoids were negligible.

The response variable used as the descriptor of rate of colonisation for the 2 algae was stolon maximum length which was measured *in situ*. During the study, the experimental units grew abundantly and the fragments transplanted at the beginning developed into patches of interlaced stolons. Hence, to estimate stolon growth we decided to measure the length of the longest stolon per patch, even if it was over the edges of the experimental unit. Percent cover of algae in experimental units would have been less informative if the growth of both species was fast, as just a few fragments could totally cover the local substratum (Piazzì et al. 2001). The response variable was measured 5 times (July, October 1998, January, April and September 1999). Data from the last sample were analysed by asymmetrical fixed factorial ANOVAs to determine differences among density treatments (amount of initial fragments and proportion of species). The required sums of squares for asymmetrical components of these analyses were calculated following Underwood (1992, 1993, 1997). Before running the analyses, the assumption of homogeneity of variances was examined using Cochran's test. Student-Newman-Keuls (SNK) tests were used for a posteriori multiple comparisons of means.

***Caulerpa taxifolia* transplant experiments.** Fragments of *C. taxifolia* were transplanted into high density *C. racemosa* patches; the reverse transplants could not be done because of the sporadic occurrence of *C. taxifolia* at the site. In each experimental plot (20 × 20 cm), 4 fragments of *C. taxifolia* were fixed to the substratum as described above. In the *C. racemosa* habitat more than 50 stolons of the alga were present, while in controls only algal turfs were present. Treatment and control experiments were replicated in triplicate in each of 2 areas randomly chosen within the study site. Stolon length and blade size of *C. taxifolia* was measured 5 times (same months as response variable measurements). Data obtained on the last sam-

Table 1. Competition experiments. Experimental treatments [1 to 10] to determine influences of inter- and intraspecific competition on blade density and stolon lengths of *Caulerpa taxifolia* (CT) and *C. racemosa* (CR) at different fragment densities

	Fragment density		
	Control (2)	(2 + 2)	(2 + 4)
<i>Caulerpa taxifolia</i>			
CT added	[1] 2 CT	[2] 2 CT + 2 CT	[3] 2 CT + 4 CT
CR added		[4] 2 CT + 2 CR	[5] 2 CT + 4 CR
<i>Caulerpa racemosa</i>			
CR added	[6] 2 CR	[7] 2 CR + 2 CR	[8] 2 CR + 4 CR
CT added		[9] 2 CR + 2 CT	[10] 2 CR + 4 CT

pling date were analysed 2-way ANOVA with 'habitat' (*C. racemosa* vs algal turfs) treated as the fixed factor and 'area' (2 levels) as the random factor nested to 'habitat'. Cochran's test was used to test the assumption of homogeneity of variances.

RESULTS

Competition experiments

Caulerpa racemosa and *C. taxifolia* stolon length was greater in October 1998 and in September 1999 than the other dates for both species. From October to January *C. taxifolia* stolon size did not change while *C. racemosa* stolon length decreased (Fig. 1). Between January and April, a decrease in stolon size was recorded in *C. taxifolia*, while a more relevant change in stolon length was observed for *C. racemosa*, which regressed to smaller sizes than the ones initially recorded.

Overall, results clearly showed that stolon length increased with respect to controls. However, this effect significantly differed among treatments. *Caulerpa taxifolia* stolon length was significantly affected by the addition of fragments (density) depending on the species added (*C. taxifolia* vs *C. racemosa*) (Fig. 1A, Table 2). This result suggests a significant interspecific effect on stolon length of *C. taxifolia* where 4 fragments were added, since a lower stolon length was recorded where *C. racemosa* was present. Conversely, in the case of 2 fragments added (2 + 2 treatments) there was not a significantly different effect between species added (Table 2, SNK test). Further, where *C. taxifolia* fragments were added to fragments of the same species, a positive effect of the increase in density was found indicating a positive intraspecific inter-

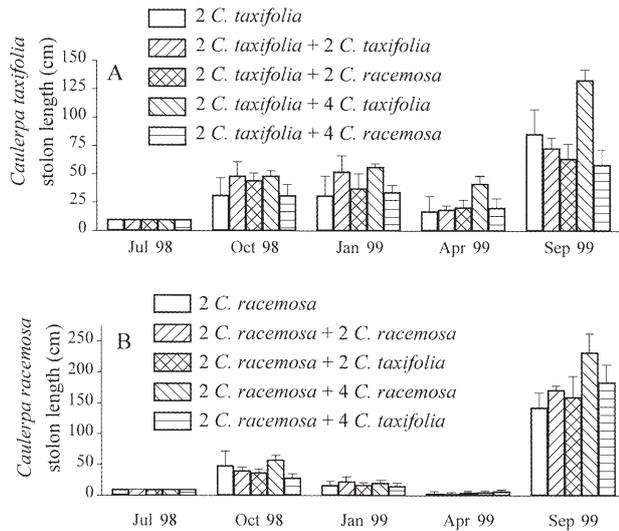


Fig. 1. Competition experiments. Temporal variation during the study period of mean (\pm SE) stolon length of (A) *Caulerpa taxifolia* and (B) *C. racemosa* in treatments of different densities and different species added ($n = 3$ replicates). Numbers reported on legend refer to fragments combinations used in treatments

action (Table 2, SNK test). Conversely, *C. racemosa* stolon length was found to be homogeneous among treatments: none of the factors significantly affected stolon size (Fig. 1B) and thus neither the density nor the species added.

***Caulerpa taxifolia* transplant experiment**

Caulerpa taxifolia showed a different temporal trend between the 2 habitats both in stolon length and blade

size (Fig. 2). For example, an increase in stolon length was observed during autumn 1998 on algal turfs, while a great homogeneity over time was observed in *C. racemosa*. At the end of the study period, significant differences ($p < 0.05$) between habitats were detected, both in stolon length and in blade size (Fig. 2) ($F_{1,2} = 292.6$ and $F_{1,2} = 102.1$, respectively). In September 1999, *C. taxifolia* stolon length was 16.7 ± 2.1 and 77 ± 4.6 cm in *C. racemosa* habitat and on algal turfs, respectively, and blade size was 5.8 ± 0.4 and 20.2 ± 1 cm, respectively. No significant difference ($p > 0.05$) was found between experimental areas for both response variables, suggesting that local conditions do not affect the algal spread ($F_{2,8} = 1.79$ and $F_{2,8} = 0.6$ for blade size and stolon length, respectively). Overall, *C. taxifolia* fragments transplanted into *C. racemosa* patches showed clear signals of stress in comparison to those transplanted into algal turfs: blades began to fade in color and branches reduced their length (Fig. 2) as evidenced since the first sampling date. This pattern was consistent over the study period.

DISCUSSION

Temporal patterns found for the stolon length of *Caulerpa taxifolia* and *C. racemosa* were in accordance to seasonal variations in stolon length and blade size shown in other studies for both algae in the Mediterranean (Meinesz et al. 1995, Ceccherelli & Cinelli 1998, Piazzini & Cinelli 1999, Ceccherelli et al. 2000). *C. racemosa* has stronger temporal fluctuations compared to *C. taxifolia*. For the former species the period of vegetative rest occurred earlier (between October and January), and during that period a more dramatic thallus reduction was found than for *C. taxifolia*.

Despite this, *C. racemosa* showed greater stolon elongation than *C. taxifolia*, as observed in previous studies (Piazzini et al. in press), which counterbalanced the winter regression. This feature suggests that the response of the 2 species to environmental changes is quite different, contrary to the initial belief that their tolerances would be very similar as they belong to the same genus and both have tropical origins.

Although interspecific effects occurred, the overall increase in stolon length at higher densities for both species suggested that positive interactions are very important. A positive intraspecific interaction was detected for *Caulerpa taxifolia*, suggesting that growth increases at higher densities. A similar

Table 2. Competition experiments. Results of asymmetrical ANOVA of the experimental treatments (Table 1) to determine inter- and intraspecific competitive interactions on *Caulerpa taxifolia* stolon length depending on density (D) of fragments and species (S) added. Cochran's tests were not significant ($C = 0.26$)

Source of variation	Stolon length			
	df	MS	F	p
Among treatments (1–5)	4	2686.9	6.82 _{4,10}	<0.05
Control (1) vs others (2–5)	1	30.7	0.08 _{1,10}	ns
Among other treatments (2–5)	3	3572.3		
Density [(2 + 4) vs (3 + 5)]	1	2214.1		
Species [(2 + 3) vs (4 + 5)]	1	5334.1		
D × S	1	3168.7	8.04 _{1,10}	<0.05
Residual	10	393.9		

SNK result of D × S. T = *C. taxifolia*, R = *C. racemosa*. SE = 11.2, df = 8

	Density	Species added	
2 + 2 fragments	T = R	T	2 + 2 < 2 + 4
2 + 4 fragments	T > R	R	2 + 2 = 2 + 4

pattern was found in *C. racemosa* even when differences among treatments were not significant. Positive intraspecific interactions have already been described for other macroalgae, which affect survival, growth and reproduction of the species. Density mostly influences plant resistance to hydrodynamism, vulnerability to grazing and dislodgement, and epiphyte growth (Schiel & Choat 1980, Hay 1981, Padilla 1984, Reed 1990). For these introduced *Caulerpa* species, the exaggeration of the negative effect of hydrodynamism is likely to be the most important mechanism of interaction. Although further experimental studies would be necessary to test this hypothesis, shelter condition has already been indicated as facilitative, even if detrimental to light availability. Lower grazing pressure seems to be the least probable positive effect of the high density of *Caulerpa* spp. as neither are subjected to significant grazing in the Mediterranean (Boudouresque et al. 1996, Ganteaume et al. 1998).

In general, competitive interactions in seaweeds may occur through both interference and exploitation mechanisms (Carpenter 1990, Olson & Lubchenco 1990); on the other hand, species have different competitive abilities in relation to their life-history traits (Gaudet & Keddy 1988). The mechanisms involved in these interactions can be consumption, pre-emption, overgrowth, or through allelochemical substances (e.g., Schoener 1983, Olson & Lubchenco 1990). The species examined in this study have very similar characteristics; they are both invasive and considered to be strong competitors (Meinesz & Hesse 1991, de Villèle & Verlaque 1995, Ceccherelli & Cinelli 1997, Ceccherelli unpubl. data). They showed similar competitive characteristics based on direct interference by overgrowth (de Villèle & Verlaque 1995, pers. obs.).

Significant interspecific effects were detected between the 2 species with the densities used in this experiment. In fact, *Caulerpa racemosa* strongly affected *C. taxifolia* stolon size (competition experiments) and blade size (*C. taxifolia* transplant experiment). Mechanisms that regulate this interaction still need to be investigated. Direct interactions such as overgrowth may be involved in competition between algae with similar characteristics. This type of competitive mechanism has been mostly described in nongeniculated Corallinales (Sebens 1986, Morcom et al. 1997) and turf-forming algae (Airoldi 2000). However, stoloniferous marine species may easily overgrow other benthic organisms (Verlaque & Fritayre 1994, Piazzini et al. 1997): the interaction between 2 stoloniferous overgrowing species, such as those of this study, is likely to be very affected by the elongation rate of stolons. Due to the rapid growth and ability to form multilayer mats (Piazzini & Cinelli 1999), *C. racemosa* stolons quickly overgrew stolons of *C. taxifolia*. This feature happened where

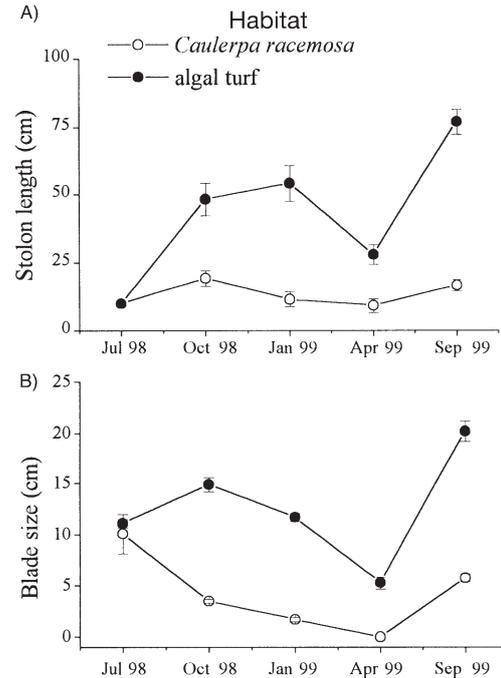


Fig. 2. *Caulerpa taxifolia* transplant experiment. Temporal variation during the study period of mean (\pm SE) of (A) *Caulerpa taxifolia* stolon length and (B) blade size on *C. racemosa* and on algal turf (n = 6 replicates)

both species were transplanted (competition experiments) and where *C. taxifolia* was transplanted into *C. racemosa* established patches (*C. taxifolia* transplant experiment). However, aboveground characteristics of the 2 species are very different: *C. taxifolia* has a much higher canopy (8 to 9 cm mean) compared to *C. racemosa* (~2 cm), which remained in the shade of the former. *C. taxifolia* canopy size prevents suffocation and shading by *C. racemosa*, even though the presence of *C. racemosa* has an effect on its blade size. Furthermore, the allelochemical mechanism of direct interaction might be involved, and in fact, the different presence of fatty acids, sterols and diterpenes among the most common species of this genus has suggested that *C. racemosa* and *C. taxifolia* are phytochemically different in many aspects (Aliya & Shameel 1998).

Exploitative mechanisms of interaction are the least probable for these algae. Being good pioneers on unvegetated sediment (Williams 1990), they have a wide range of tolerance and are not affected by nutrient and light limitation (Chisholm et al. 1996, Delgado et al. 1996, Ceccherelli & Cinelli 1999b). *Caulerpa* can uptake nutrients using rhizoids (Williams 1984), and thus nutrient availability in the sediment should affect both species since they exhibit similar rhizoid morphology (Ceccherelli & Cinelli 1997). The fact that species blade size is different should favour the

resource acquisition of *C. taxifolia* as this species is otherwise less advantaged from the outcome of the interaction.

Overall, the results of this study suggest that growth increases with density augmentation especially in *Caulerpa taxifolia*. Therefore, this result suggests that invasive characteristics of the species may increase with time of colonisation. Rate of colonisation, although initially quite high during invasion when isolated fragments establish, tends to increase at higher densities. In general, based on the interspecific effects observed, we predict that where both species co-occur *C. racemosa* would be the favoured species in the outcome of the competition.

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