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NOTE

Habitat effect on spatio-temporal variability in size and density of the introduced alga *Caulerpa taxifolia*

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ABSTRACT: *Caulerpa taxifolia* is an introduced green seaweed in the Mediterranean; it is a very fast-spreading species, is able to invade all kinds of substrata and causes regression of some seagrasses. *C. taxifolia* was investigated in a small bay of the northwestern Mediterranean, where it occupies 3 distinct habitat types: (1) at the edge of *Posidonia oceanica*, (2) within *Cymodocea nodosa* beds, and (3) on sand and cobbles. To provide a basis for further experimental investigations of the factors affecting its performance, a descriptive study was carried out at this site in which both size and density of blades were measured on 20 dates in all habitats from October 1994 to September 1996. Great temporal fluctuations within the same season were evident for both variables, despite the fact that high variability was found at small spatial and temporal scales (areas within each habitat and time within each season). However, habitat effect in combination with season was evident as a major factor affecting both length and density of blades, suggesting a positive effect of seagrasses on *C. taxifolia*. The greatest blade length was found in individuals at the edge of *P. oceanica*, while within *C. nodosa* beds, blade length was intermediate. Reduction of blade density occurred in spring in the sand and *C. nodosa* habitats, but not in the *P. oceanica* one. Patterns were similar throughout the 2 years. Experimental evidence is needed both to highlight mechanisms regulating this kind of interaction (nurse effect vs shade-induced changes) and to investigate whether it affects patterns of invasion and replacement of existing species with *C. taxifolia* in these habitats. The facilitative effect of seagrasses on the alga observed in this study is also likely to cause an indirect negative effect on seagrasses themselves.

KEY WORDS: *Caulerpa taxifolia* · Habitat modification · Introduced alga · Seagrasses

One of the major goals of community ecology is to understand the factors that generate patterns in natural communities. The ecological performance of sessile organisms, both plant and animal, must be dependent primarily on localized site features and most of them may be found in a variety of habitat types, even within a relatively small spatial scale. As a result, individuals in different local subpopulations of the same species may experience different probabilities of survival and reproduction, depending on which habitat they occupy (e.g. Fowler 1984, Kadmon 1993). Many seaweeds are known for their remarkable variation in morphology both between and within populations, and this trait likely allows them to grow in a wide variety of habitats and conditions (e.g. Taylor & Hay 1984, Molloy & Bolton 1996).

Occurrence of non-indigenous species is increasing in coastal areas around the world (Carlton 1989, Carlton & Geller 1993, Lodge 1993). Some of these species not only successfully establish themselves, but profoundly change the biodiversity in their new environment. An important goal is to detect the determinants of distribution and abundance of a potential invader and of vulnerability to invasion for different communities.

In the Mediterranean, the tropical seaweed *Caulerpa taxifolia* (Vahl) C. Agardh was found for the first time in 1984 along the French coast, and since then, it has been invading wide areas of the basin, behaving as a highly successful, fast-spreading species (Boudouresque et al. 1992, Meinesz et al. 1993). *C. taxifolia* occurs on a variety of surfaces: it can colonize muddy and sandy sediments, cobbles, and even hard substrata. At present it is known to impact seagrasses of the Mediterranean such as *Posidonia oceanica* (de Villèle & Verlaque 1995) and *Cymodocea nodosa* (Ceccherelli & Cinelli 1997), causing their decay and regression.

Commonly, competitive and facilitative interactions between plants are known to directly influence their morphology and physiology (Ehleringer 1984, Bertness & Hacker 1994, Callaway 1994, Hacker & Bertness 1996) as well as patterns of distribution and abundance (Dayton 1975, Harper 1977, Fowler 1986, Tilman 1988).

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The presence of neighbours can alter the physical conditions of the substrate. Within seagrass habitats, as suggested by de Villèle & Verlaque (1995), rhizomes likely represent a highly suitable substratum for the progression of *Caulerpa taxifolia*. In general the physical and chemical conditions of the substratum likely play a major role in algal growth; for example, rhizophytic algae, such as Caulerpales, can take up nutrients from the sediment through rhizoids and translocate them to the blades (Williams 1984). Experimental evidence has also suggested that enrichment of nutrient availability in the sediment determines the increase of algal density (Ceccherelli & Cinelli 1997). In addition, the presence of neighbours can alter physical conditions of the aboveground component. For example, seagrasses create a peculiar habitat for understory algal species because of canopy shading, reduction in water motion (Gambi et al. 1989, 1990), and production of secondary metabolites that can allelopathically interfere with them and grazers (Cuny et al. 1995).

This descriptive study focuses on patterns of spatial and temporal variation in size and density of *Caulerpa taxifolia* blades in 3 different habitat types: at the study site *C. taxifolia* occurs in monospecific stands on sand and cobbles, interspersed within a *Cymodocea nodosa* bed and at the edge of *Posidonia oceanica* patches. The aim of this study is to provide a basis for further experimental investigations of the factors affecting the performance of this alga in the Mediterranean.

Table 1. *Caulerpa taxifolia*. Results of multifactorial ANOVA on blade length: H = Habitat; S = Season; T = Time; A = Area. Although data were square-root transformed, Cochran's test was slightly significant ($C = 0.0500$, $p < 0.05$). According to Underwood (1981) the effect of Habitat × Season was tested over the pooled term Habitat × Time(S) + Season × Area(H) + Area(H) × Time(S). Bold type indicates significance ($p < 0.05$). SNK test: Cy = *Cymodocea nodosa* habitat, Sa = sand and cobbles habitat, Po = *Posidonia oceanica* habitat; Su = summer, Au = autumn, Wi = winter, Sp = spring; df = 115 and SE = 0.10. SNK test was not performed on the A(H) × T(S) interaction because this involves random factors that do not test for any specific hypothesis. Thus, identifying a particular ordering of levels would add nothing to the results of the *F*-test

Source of variation	df	MS	*F*	p
Habitat = H	2	40.233[a]		
Area(H) = A	9	0.729	1.53	0.1545
Season = S	3	55.937[a]		
Time(S) = T	8	2.168	4.54	**0.0001**
H × S	6	0.989	2.10	0.0588•
H × T(S)	16	0.598	1.25	0.2503
S × A(H)	27	0.382	0.80	0.7344
A(H) × T(S)	72	0.477	3.94	**0.0000**
Error	432	0.121		
•Pooled term	115	0.472		

[a] Factors not tested because an appropriate denominator was lacking

SNK test of Habitat × Season term

Habitat	Season	Season	Habitat
Po	Su = Au > Wi > Sp	Au	Po > Cy > Sa
Sa	Su = Au > Wi > Sp	Wi	Po > Cy > Sa
Cy	Su = Au > Wi > Sp	Sp	Po = Cy = Sa
		Su	Po > Cy > Sa

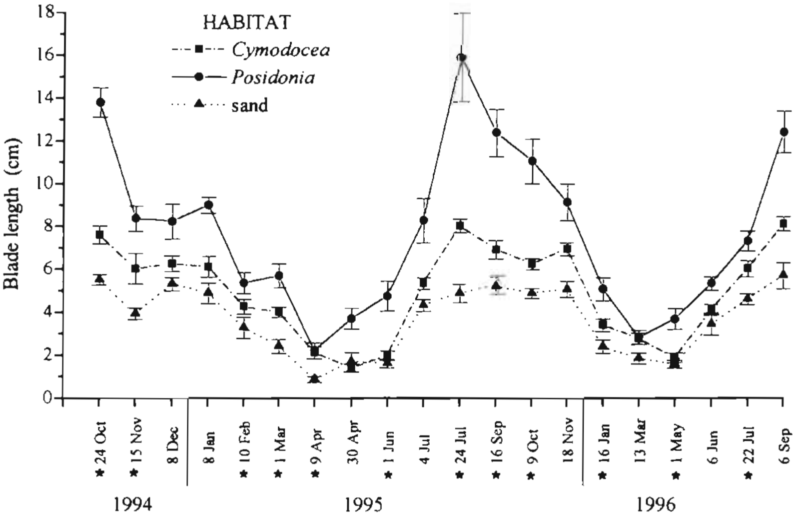

Fig. 1. *Caulerpa taxifolia*. Temporal changes in mean blade length (± 1 SE) during the study period in the 3 habitats (*Posidonia oceanica*, *Cymodocea nodosa* and sand/cobbles). Each value represents the mean of 16 observations (4 replicates in each of the 4 areas). Asterisks refer to data analysed

Methods and results. The study site is a shallow subtidal seagrass bed composed of a continuous bed of *Cymodocea nodosa* and few small patches of *Posidonia oceanica* in 1 m water depth, located in Galenzana Bay on the south coast of Elba Island, Italy (42° 43' N, 10° 14' E). Since July 1993, when *Caulerpa taxifolia* was first discovered here, the alga has been invading this area, successfully occupying the habitats mentioned above.

This study was done over 2 years (from October 1994 to September 1996): samples were taken on sets of 3 dates randomly chosen within each season across the study period, although on 4 dates sampling was not possible because of weather conditions. Density and size (length) of blades measurements were obtained by sampling, for each habitat, 4 areas randomly chosen out of 8 and ranging in size from 2 to 4 m^2. The 3 habitats are not spatially segregated and the 12 areas chosen for sampling were interspersed within the bay. Blade length of *Caulerpa taxifolia* was measured *in situ* from the stolon level using a plastic calliper, while a 10 × 10 cm sampling square was used to estimate blade density. For both variables 4 randomly chosen replicates were sampled in each area. The whole study was performed in a 3000 m^2 site.

To analyse data for both response variables, 3 sampling times within each season were randomly chosen out of all those available; those used for analysis are indicated in Figs. 1 & 2. Data were analysed using 4-way ANOVAs (Statistica 1994). The factors tested were: 'habitat' and 'season' treated as fixed factors, and 'time' and 'area', treated as random and respectively nested in the season and habitat terms. Cochran's test was performed to check for homogeneity of variance and although transformation of data was performed, the test was slightly significant for blade length; results were judged reliable for the extremely high number of degrees of freedom. An SNK multiple comparison test was used to identify alternative hypotheses.

Blade length was greatly affected by habitat type: for the whole study period *Caulerpa taxifolia* had the longest blades at the edge of *Posidonia oceanica* patches and shortest on the sand and cobbles, while the intermediate size occurred in individuals interspersed within *Cymodocea nodosa* (Table 1, Fig. 1). Although differences among habitats were not significant during spring, *C. taxifolia* at the edge of *P. oceanica* was significantly taller than in the other habitats during all other seasons (Table 1, SNK test). In summer 1995, when mean values differed most, blade length in *P. oceanica* and *C. nodosa* habitats were respectively 226.1 and 64.9% greater than in the habitat of sand and cobbles. Seasonal fluctuations, even if more pronounced in the *P. oceanica* habitat, were evident in all the habitats and similar between the years, minimum size was found in early spring (April), while maximum was observed in summer, and the SNK test identified significant ranking of seasons for all the habitats.

Table 2. *Caulerpa taxifolia*. Results of multifactorial ANOVA on blade density. Cochran's test showed variance homogeneity ($C = 0.0357$, $p > 0.05$). Bold type indicates significance ($p < 0.05$). SNK test: df = 27 and SE = 1.99. SNK test was not performed on the A(H) × T(S) interaction because this involves random factors that do not test for any specific hypothesis. Thus, identifying a particular ordering of levels would add nothing to the results of the *F*-test. Abbreviations as in Table 1

Source of variation	df	MS	*F*	p
Habitat = H	2	4046.46[a]		
Area(H) = A	9	140.37	1.06	0.4010
Season = S	3	1067.47[a]		
Time(S) = T	8	177.20	1.34	0.2377
H × S	6	628.35	3.30	**0.0144**
H × T(S)	16	165.50	1.25	0.2520
S × A(H)	27	190.32	1.44	0.1123
A(H) × T(S)	72	132.17	2.41	**0.0000**
Error	432	54.90		

SNK test of Habitat × Season term

Habitat	Season	Season	Habitat
Po	Au = Wi = Su = Sp	Au	Sa = Cy = Po
Sa	Sp = Wi = Su = Au	Wi	Sa < Cy = Po
Cy	Sp < Wi = Au = Su	Sp	Cy = Sa < Po
		Su	Sa = Cy = Po

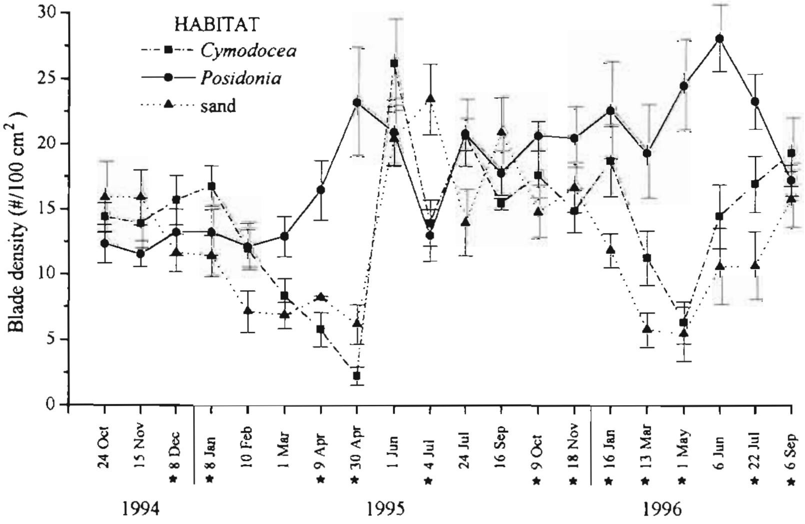

Fig. 2. *Caulerpa taxifolia*. Temporal changes in mean blade density (± 1 SE) during the study period in the 3 habitats (*Posidonia oceanica*, *Cymodocea nodosa* and sand/cobbles). Each value represents the mean of 16 observations (4 replicates in each of the 4 areas). Asterisks refer to data analysed

Blade density of *Caulerpa taxifolia* underwent great fluctuations through the seasons depending on habitat type (significant habitat × season interaction; Table 2). For 1995 and 1996, there were lower densities during spring in the *Cymodocea nodosa* and sand/cobbles habitats, while no reduction was observed in the *Posidonia oceanica* habitat (Fig. 2). In fact, in this last habitat the largest increase in blade density was observed greatly in advance (March) of that for the other habitats. Analysis identified a significantly greater blade density at the edge of *P. oceanica* during spring and a significantly lower density on sand and cobbles in comparison with seagrass habitats during winter (SNK test, Table 2). Density results were very similar among all habitats during autumn and summer.

Temporal inconsistencies were also evident at a small spatial scale for both variables, as there were significant differences among area × time combinations (Tables 1 & 2).

Discussion. Results of this study showed that both density and length of *Caulerpa taxifolia* blades greatly fluctuated in relation to seasonal period, and this is in accordance with Meinesz et al. (1995) who found similar temporal changes for meadows of the eastern side of Cap Martin in France.

Altogether, the results of this study indicate that seagrass habitats may greatly influence morphology and abundance of *Caulerpa taxifolia*. In fact, blade size of *C. taxifolia* is tightly related to the habitat type and, although the greatest differences were found during summer, for the whole study period blades of larger size were found in the *Posidonia oceanica* habitat, those of intermediate size in the *Cymodocea nodosa* habitat, while the smallest in size were found in monospecific stands of alga on sand and cobbles. Conversely, results obtained for blade density highlighted a dependence on habitat type mostly during spring when this parameter decreased in all the habitats except in *P. oceanica*, while a high spatial heterogeneity on a small scale prevailed for the rest of the year. Altogether, our observations suggest a positive effect of seagrasses, mostly of *P. oceanica*, on this rhizophytic alga.

Positive interactions are defined as those that positively influence one of the species. Usually they prevail in extreme physical conditions when a species buffers the potential physical effects limiting a neighbour (Bertness & Callaway 1994). In fact, within plant assemblages, neighbouring plants can ameliorate environments for other plants that in isolation would have to adjust to harsher physical conditions (Bertness & Hacker 1994, Callaway et al. 1996).

The performance of *Caulerpa taxifolia* in the habitats investigated could be due to the different conditions of both light and flow dynamics in the aboveground compartment. The seagrass canopy is commonly known to shade understory species and although *C. taxifolia* has been suggested to be well adapted to the light regime typical of the infralittoral and upper circalittoral zone of the Mediterranean, with no photoinhibition under high photon flux densities, photosynthetic assays indicate that it also behaves as a shade-adapted plant because of low compensation irradiance, low saturation irradiance and high efficiency of low incoming irradiances (Gacia et al. 1996). Although seasonal light requirements of this alga have been given, no mechanism of acclimation and adaptation of *C. taxifolia* to low light conditions has ever been investigated (Gacia et al. 1996). In fact, shade-induced changes of length and biomass proportions have been described for numerous terrestrial plants and aquatic macrophytes (Barko et al. 1982, Goldsborough & Kemp 1988), and we believe that blade elongation, the most obvious and dramatic morphological response of *C. taxifolia* to seagrass habitats, could represent a response to lower irradiances. An experimental study that has been carried out at the site has already indicated that the removal of the canopy of *Cymodocea nodosa* results in lower blade size of the alga (Ceccherelli & Cinelli 1997).

However, seagrasses, as well as macroalgal beds, also strongly affect hydrodynamics by bending when a current or wave passes, so deflecting the flow over or around vegetation, and by extracting fluid momentum (Fonseca et al. 1982, Madsen & Warnke 1983, Fonseca & Fisher 1986, Gambi et al. 1990). A large variety of organisms of the benthic fauna, especially juvenile stages, show preference for this microhabitat and find shelter in seagrass meadows that are for this reason defined as 'nurseries'. This phenomenon has also been found in *Posidonia oceanica* beds where low-energy microenvironments are created and deposition of suspended material is enhanced (Gambi et al. 1989). However, to our knowledge, in these particular habitats no positive interaction has ever been recognized in algal species, and its experimental demonstration would highlight new ecological perspectives.

Facilitative interactions can also occur indirectly if one competitor significantly reduces the probability that a second will be excluded from the community through high rates of predation, independent of abiotic conditions (e.g. Hay 1986). However, in the Mediterranean this facilitative mechanism on the alga is very unlikely to occur since *Caulerpa taxifolia* doesn't seem to be a valuable food source because of both the lack of direct observations of grazing (pers. obs.) and investigations of feeding on this alga by major autochthonous herbivores (Boudouresque et al. 1996).

The evidence that individuals of the alga occurring in the same habitat (i.e. at the edge of patches of *Posidonia oceanica*) and at more sheltered deeper sites (10 m) showed much larger blade size than individuals grown at more exposed shallower sites (2 m) (Ceccherelli & Cinelli unpubl.), could support a positive effect of either a reduction in irradiance or water flow protection on *Caulerpa taxifolia*. Unfortunately, shelter and sciaphylous conditions are frequently bound together in nature, because of the lack of transparency of both sheltering species and objects. Future experimental investigations will be conducted to test for the potential importance of *P. oceanica* nurse seagrass in structuring populations of the alga in the field with 'imitation' nurse plants.

Also, conditions in the sediment seem to be an important regulator of the performance of the alga in the Mediterranean. In fact, experimental evidence in the *Cymodocea nodosa* habitat carried out at the site shows that nutrient supply in the sediment plays a major role in the outcome of the competitive interaction between the 2 species (Ceccherelli & Cinelli 1997). These results, together with those obtained in this study, were unexpected since Caulerpales have been reported to be good colonizers of unvegetated sediments that are not nutrient stabilized (Williams 1990), thus suggesting that the habitat of sand and cobbles would have been the most suitable to the *Caulerpa taxifolia* growth.

Further studies will highlight the mechanism regulating the positive effect on the alga of both seagrasses and should also verify the consistency of patterns observed in this study at sites of different depths. Unfortunately, at the study site, *Caulerpa taxifolia* occurs only in very shallow and sheltered areas and we predict that the effect of seagrasses on the alga is greatly affected by different irradiance and water flow regimes existing at the deeper sites. Mechanisms that regulate this kind of interaction will provide valuable information since they are likely to affect patterns of invasion and replacement of *C. taxifolia* in these habitats. In general, a phenomenon that has not received much attention, however, is the observation that in alien environments plants tend to be more vigorous and taller (Crawley 1987). *C. taxifolia* in the Mediterranean is much greater in size than in tropical habitats and has become a canopy-forming species having a major impact on autochthonous flora (Verlaque & Fritayre 1994). Indications of the ability of this alga to outcompete seagrasses have already been given (de Villèle & Verlaque 1995, Ceccherelli & Cinelli 1997), and the facilitative effect of the seagrasses on algal growth can represent an indirect negative effect on the seagrasses themselves.

To interpret results about the performance of *Caulerpa taxifolia* in the Mediterranean correctly, it is necessary to perform well designed experiments, because of the high variability on a small spatial scale as shown in both variables investigated in this study.

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