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NOTE

The role of vegetative fragmentation in dispersal of the invasive alga *Caulerpa taxifolia* in the Mediterranean

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ABSTRACT: This study evaluated the importance of fragmentation in the recruitment of the fast-spreading, introduced green alga *Caulerpa taxifolia* at the margins of beds of the seagrass *Posidonia oceanica*. A multifactorial experiment was designed to test the hypotheses that there are seasonal differences in patterns of establishment of vegetative fragments, whether this process changes with depth and whether these patterns were consistent at different spatial and temporal scales. Our experimental approach consisted of dispersing drifting fragments of *C. taxifolia* along the margin of a bed of *P. oceanica* and recording the number of fragments established after 1 mo. The results show that a surprisingly large number of fragments become established in this habitat and that numbers varied in space and time: the probability of establishment of fragments was greatest during summer especially at the shallow sites, but smaller in spring and smallest in winter. Differences among areas were also found: a great variability in establishment of fragments depended on the site and time within season. Results indicate that dispersal by fragmentation can greatly contribute to a very wide spread of the alga in the Mediterranean. We predict that spread will be greatest during summer when a large proportion of fragments can re-attach to the substratum, even at shallow sites. Such information is important for the understanding of the ecology of this species and, with the help of hydrographic studies, in the prediction of its patterns of geographic dispersal.

KEY WORDS: *Caulerpa taxifolia* · Dispersal · Vegetative reproduction · Introduced alga · Fragmentation · Colonisation

Biological invasions are a great threat to the integrity of natural communities of plants and animals and to the preservation of endangered species (Carlton & Geller 1993). Despite growing concern over the negative effects of such invasions, we still know surprisingly little about the determinants of distribution and abundance of invading plant species at local or regional scales (but see Richardson & Bond 1991, Williams & Black 1994, Trowbridge 1995, Rejmánek & Richardson 1996, Thébaud et al. 1996). In general, the limits to invasion are provided by many processes, such as the life-history of the invader, including mode of reproduction, growth rate and dispersive capability (Elton 1958, Ashton & Mitchell 1989, Trowbridge 1995, Andrew & Viejo 1998). Recent data on biological invasions show that expansion of range is driven by various modes of dispersal, such as the neighbourhood diffusion and long-distance dispersal that can occur within a species (Shigesada et al. 1995). Although numerous reports have documented the 'patterns of spread' of non-indigenous species, we have virtually no detailed studies regarding the mechanisms of spread for any large-scale invasion (Johnson & Carlton 1996) and predicting the spread of introduced species has been a challenging task for ecologists.

Caulerpa taxifolia (Vahl) C. Agardh is a fast-spreading introduced, species in the Mediterranean (Meinesz & Hesse 1991, Boudouresque et al. 1992, Meinesz et al. 1993) that has created great concern in recent years. Regardless of how it was initially introduced into the Mediterranean, its subsequent rapid expansion over the last 15 yr has led to a dramatic increase in the number of permanent populations mostly along the French and Italian coasts. A chronology of the establishment of *C. taxifolia* was reported by Boudouresque et al. (1994) and Meinesz et al. (1998).

Caulerpa taxifolia exhibits typical features of an invasive weed, having high productivity (Gacia et al. 1996), high tolerance (Gayol et al. 1995, Delgado et al. 1996, Sant et al. 1996, Komatsu et al. 1997) and due to its reproductive modality. Furthermore, it is capable of reproducing sexually or asexually; however, in the Mediterranean, production of gametes has never been observed and only asexual reproduction is considered to contribute to its spread (Pou et al. 1993). Asexual reproduction is generally considered to be the most

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important. It occurs in 2 ways: (1) by vegetative growth or patch expansion and (2) by fragmentation, dispersal and re-establishment of drifting fragments (Fradà-Orestano et al. 1994). *C. taxifolia* clones are fragmented naturally or as a consequence of human activities. Wave action in shallow habitats and human impact caused by boat propellers, anchors, and professional and recreational fishing activities in meadows of the alga can be important sources of fragmentation. Detached fragments may then drift away and be dispersed to other habitats. Theoretically, all fragments of *C. taxifolia* have the potential to establish (Jacobs 1994). Observation of fragments that are naturally and accidentally uprooted has, however, shown that they often consist of all the portions of the thallus (i.e. blade, stolon and rhizoid). If re-establishment is frequent, fragmentation could be an important method of dispersal and colonisation of new areas.

Although many aquatic plants predominantly disperse by vegetative means (Johansson & Nilsson 1993, Barrat-Segretain 1996, Barrat-Segretain et al. 1998), little work has been done on the ecological significance of dispersal and colonisation (Titus & Hoover 1991). Furthermore, abilities of the fragments to regrow (regeneration) and their potential for establishment (colonisation) have not been well documented (Barrat-Segretain et al. 1998).

The introduced alga *Caulerpa taxifolia* in the Mediterranean is able to colonise seagrass meadows from the margins and to exert negative effects on seagrasses (de Villèle & Verlaque 1995, Ceccherelli & Cinelli 1997, 1998). The objective of this paper was to determine the importance of fragmentation in recruitment of *C. taxifolia* at the margin of beds of the seagrass *Posidonia oceanica*. A multifactorial experiment was designed to test (1) the hypothesis that there are seasonal differences in patterns of establishment of algal fragments, (2) the hypothesis that establishment differs with depth, and (3) the hypothesis that patterns were consistent at different spatial and temporal scales. Such information may be important for understanding the ecology of this species and to predict its patterns of dispersal.

Methods. This study was carried out in Galenzana Bay on the south coast of Elba Island, Italy (42° 43' N, 10° 14' E), from October 1995 until September 1996. To assess the natural establishment of *Caulerpa taxifolia*, we released fragments of plants similar in size to those detached naturally at the site. On 3 dates randomly chosen within each season, 20 fragments 15 cm long with stolon, blades and rhizoids were manually uprooted from the same habitat (at 1 m depth on sand) and dispersed along replicated margins (each 3 m in length) of a *Posidonia oceanica* bed in areas not colonised by the alga, approximately 50 to 150 m away from natural beds of *C. taxifolia*. On each date, 20 fragments were spread at each of the 3 replicate margins in each of 2 areas randomly chosen at each of 2 depths (3 m and 10 m).

The number of fragments established along the seeded margins were recorded after 1 mo, a reasonable period to ensure that the establishment and loss of fragments would both have occurred. No natural colonisation was observed in unseeded areas around the experimental ones and, by the end of the experiment, colonisation of the margins of *Posidonia oceanica* meadow had occurred exactly where fragments were placed, possibly because, in this sheltered Bay, water flow is predominantly inwards and the experimental areas were outside the established *Caulerpa taxifolia* meadows.

A 4-way ANOVA of the proportion of fragments established was performed: 'Depth' and 'Season' were treated as fixed factors, while 'Area' and 'Time' were random. Depth and Season were considered orthogonal, while Time was nested in Season, and Area was nested in a combination of Depth × Time. Where appropriate, SNK procedures were used to separate means that differed significantly in ANOVA. Cochran's test was used prior to the ANOVA to test the assumption of homogeneity of variances.

Results and discussion. Propagation through vegetative fragments should be considered an important mode of asexual reproduction of *Caulerpa taxifolia*, contributing to a net gain of population spread. The patterns of re-establishment of fragments changed with

Table 1. *Caulerpa taxifolia*. (A) Results of ANOVA on the proportion of fragments established (significant results are given in **bold**). Cochran's test was not significant after transformation (C = 0.15, p > 0.05). (B) SNK test of the factor 'Depth × Season': WIN = winter; SPR = spring; SUM = summer; AUT = autumn. SE = 0.025, df = 8

(A) ANOVA

Source of variation		df	MS	*F*	p
Depth	= D	1	0.126		
Season	= S	3	2.210		
Time(S)	= T	8	0.352	11.03	**0.0000**
Area(T(S)×D)	= A	24	0.032	2.34	**0.0019**
D × S		3	0.518	4.63	**0.0369**
D × T(S)		8	0.011	0.35	0.9361
Error		96	0.014		
Transformation:		$x^{1/2}$			

(B) SNK test

Depth (m)	Seasons	Season	Depth
3	SUM > SPR > AUT = WIN	SUM	3 m > 10 m
10	SUM > SPR = AUT = WIN	AUT	3 m = 10 m
		WIN	3 m = 10 m
		SPR	3 m > 10 m

season and the magnitude of the differences changed with depth, resulting in a significant interaction of Depth × Season (Table 1, Fig. 1). The probability of re-establishment of fragments was greater in summer at the shallow site than in the other seasons and in deep water. Approximately 37% of fragments established in summer, 15% in spring, 6% in autumn, while only 1% were established in winter (Fig. 1). The number of fragments of *C. taxifolia* established at the 10 m and 3 m deep sites varied from 0 to 20 and from 0 to 18 replicate^{-1}, respectively. During summer and spring, the numbers of established fragments were greater at 3 m than at 10 m (Table 1, SNK) which suggests that (1) light could have acted as a positive factor, since about 59 and 23% of surface light irradiance was found at the shallow and deep sites, respectively, or (2) water flow even in the calm regime, at about 2.5 cm s^{-1}, could have reduced establishment (Ceccherelli & Cinelli unpubl. data).

The season of maximal production of fragments could differ from the optimal season for establishment. Also, it is likely that fragments are mainly produced in summer by human activity, while the winter-autumn-spring fragments are caused by natural disturbances. However, although it seemed consistent throughout the seasons (Ceccherelli pers. obs.), fragment population was not quantified at the study sites.

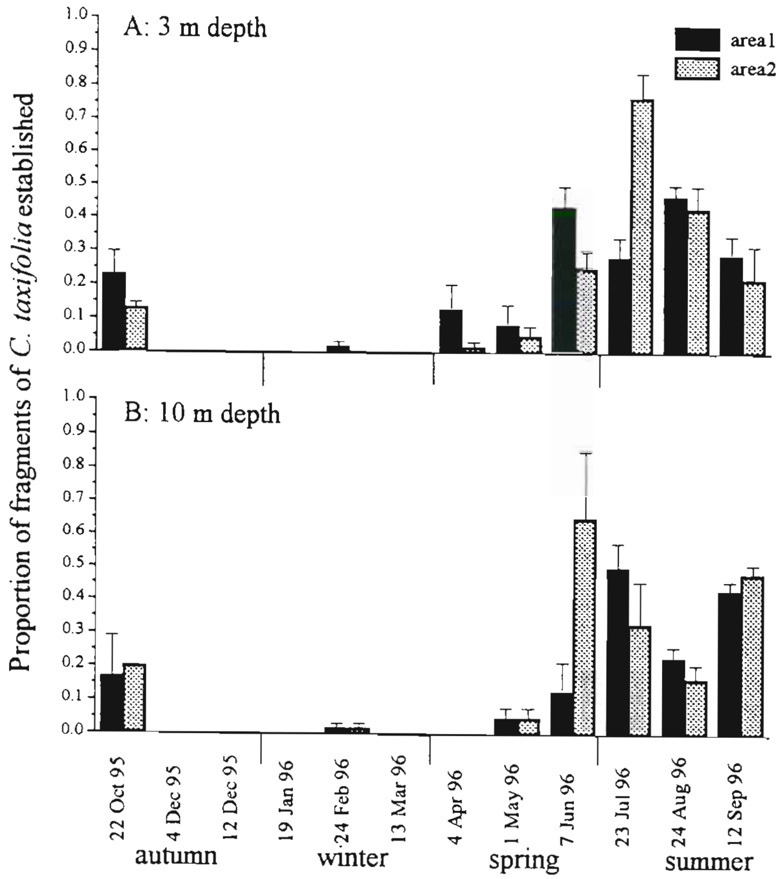

Fig. 1 *Caulerpa taxifolia*. Mean proportion (+SE) of the number of fragments established at the margin of *Posidonia oceanica*, dispersed 3 times in each season at 2 different depths (3 and 10 m). For each treatment, data for each area are shown

There was considerable small-scale spatial and temporal variability in patterns of establishment of fragments, suggesting that re-attachment of *Caulerpa taxifolia* to the substratum is affected by processes that differ from one area of the substratum to another and with depth (Area (T(S) × D) significant interaction, Table 1). Many factors can determine small-scale spatial heterogeneity in establishment of fragments, including the texture of the substratum and the supply of nutrients, both of which are likely to be important regulators of the performance of the alga in the Mediterranean (Ceccherelli & Cinelli 1997). Furthermore, the presence of turf-forming algae (such as the introduced Rhodophyta *Acrothamnion preissii* [Piazzi et al. 1996] which commonly colonises *Posidonia oceanica* rhizomes at the study site), has the potential to influence the establishment of *C. taxifolia* through physical trapping. In this experiment, we found many more re-attached fragments where the substratum was covered by algal turfs.

Ambient conditions, either spatial (area) or temporal (meteorological), could act in concert with morphological characteristics of the alga to influence the probability of establishment of fragments. In this experiment, we tested the potential for establishment only for fragments of *Caulerpa taxifolia* composed of stolon, blade and rhizoid. Establishment of single portions or different-sized fragments has not been examined. Also, drifting after detachment could change the morphology by deterioration of the fragments; this may determine the fate of colonisation. *In situ* survival of drifting fragments could not be assessed because neither tagging and marking of the dispersed fragments nor a subsequent census of them was possible. Hence, we were not able to find out the fate of fragments that were lost from the seeded areas, whether they become established elsewhere and at what distance from the source.

The potential importance of fragments in the dispersal of *Caulerpa taxifolia* has already been emphasised.

Observations from a submarine by Belsher & Meinesz (1995) indicated that the alga was present either as drifting fragments or as fixed plants at depths of 45 to 100 m off the most densely invaded coast near Monaco. These authors suggested that the local downward dispersal of the tropical alga could be attributed to the detachment of fragments. Sant et al. (1996) found that fragments of this alga could survive for several days in dark and humid conditions. They suggested that transportation of fragments by boat could be an important route of dispersal.

The spread of other invasive algae has been imputed to the drifting of fronds; for example, drifting fragments of *Sargassum muticum*, although they can reattach to the substratum, can continue to grow and become fertile so that every single branch can release numerous progenies over a very long-distance range (Rueness 1989 and references therein).

With regard to the spread of *Caulerpa taxifolia* in the Mediterranean, we conclude that the estimation of the strong establishment ability of fragments (this study), in combination with results obtained by Belsher & Meinesz (1995) and Sant et al. (1996), which suggest the presence of drifting fragments even in deep sites and resistance to desiccation, respectively, indicates that the horizontal and vertical dispersal of *C. taxifolia* meadows by fragmentation and the establishment of new colonies is possible. Although fragmentation by human activity of existing colonies of *C. taxifolia* could be avoided, by preventing anchoring and fishery activities, dispersal by fragmentation due to natural disturbance could still contribute to a very wide spread of the alga in the Mediterranean. Despite frequent wave surges throughout all seasons, we predict that the most dangerous production of fragments will occur during summer and that a large proportion of fragments can re-attach to the substratum even at shallow sites. Based on this reproductive strategy of *C. taxifolia*, hydrographic studies could help to explain geographical patterns of dispersal. Analysis of the genetic structure of invading populations may provide an additional test of the hypothesis that invasion by *C. taxifolia* is mainly a consequence of vegetative propagation.

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