

Alterations of the structure of *Posidonia oceanica* beds due to the introduced alga *Caulerpa taxifolia*

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SUMMARY: The impact of *Caulerpa taxifolia* on the structure of shallow *Posidonia oceanica* beds was studied in permanent quadrats from 1995 to 2005 at the invaded site of Cap Martin and the control site of Cap d'Antibes (French Riviera, France). The cover of *C. taxifolia*, shoot density, number of orthotropic and plagiotropic shoots and proportion of ramifications of *P. oceanica* were measured yearly. The cover of *C. taxifolia* in the invaded zone rapidly reached a maximum of infestation in 2000 with 93% of the quadrats covered by the alga. In 2001 an unexplained phenomenon led to a sharp decrease in the infestation and in the following years the colonisation remained low. Within the 10 years of the study, *P. oceanica* did not disappear from the permanent quadrats, but we observed a drastic change in the structure of the meadow invaded by *C. taxifolia*. Between 1999 and 2000 a decrease in the shoot density observed at both sites was probably related to the warm temperature event recorded in 1999 (from 636 to 143 shoots m⁻² at the invaded site and from 488 to 277 at the control site). At the invaded site, the seagrass never recovered its initial density even after a sharp decrease in *C. taxifolia*. The orthotropic/plagiotropic shoot ratio was strongly modified at the invaded site, where plagiotropic shoots became dominant because of an increase in their ramification.

Keywords: *Caulerpa taxifolia*, *Posidonia oceanica*, competition, ecological impact.

RESUMEN: ALTERACIONES EN LA ESTRUCTURA DE PRADERAS DE *POSIDONIA OCEANICA* DEBIDO AL ALGA INTRODUCIDA *CAULERPA TAXIFOLIA*. – El impacto de *Caulerpa taxifolia* sobre la estructura de la comunidad de *Posidonia oceanica* poco profunda se estudió entre 1995 y 2005 mediante parcelas permanentes en una zona invadida de Cap Martin y una zona control en Cap d'Antibes (Riviera Francesa, Francia). Para ello, se midieron anualmente la densidad de *C. taxifolia*, y la densidad de haces, el número de haces ortotrópicos y plagiotrópicos y la proporción de ramificaciones de *P. oceanica*. La densidad de *C. taxifolia* en la zona invadida alcanzó un máximo en 2000, con una cobertura del 93%, y a partir del año 2001 disminuyó drásticamente, dejando valores relativamente bajos en los años siguientes. Durante los 10 años de estudio, la pradera de *P. oceanica* no desapareció en las zonas invadidas por *C. taxifolia*, aunque se observaron cambios drásticos en su estructura. En 2000, se observó una disminución en la densidad de haces de *P. oceanica*, coincidiendo con la máxima cobertura de *C. taxifolia* (de 636 a 143 haces m⁻² en la zona invadida y de 488 a 277 en la zona control). Entre 1999 y 2000 en los dos sitios se observó una disminución de la densidad probablemente relacionada con las altas temperaturas registradas en 1999. La densidad de haces de *P. oceanica* no recuperó los valores iniciales, incluso después de la disminución de *C. taxifolia*. La relación de ejes ortotrópicos y plagiotrópicos se modificó drásticamente en las parcelas invadidas por *C. taxifolia*, donde la proporción de haces plagiotrópicos aumentó debido a un aumento de sus ramificaciones.

Palabras clave: *Caulerpa taxifolia*, *Posidonia oceanica*, competencia, impacto ecológico.

INTRODUCTION

The endemic seagrass *Posidonia oceanica* (Linnaeus) Delile constitutes one of the main coastal ecosystems of the Mediterranean Sea, forming dense

extensive meadows from the surface down to 30-40 m depth (Hartog, 1970; Boudouresque *et al.*, 2006). This ecosystem hosts a high biodiversity and plays an important role in many geomorphological and ecological processes (Boudouresque *et al.*, 2006).

Throughout most of the Mediterranean Sea, *Posidonia oceanica* is suffering constant pressure from both natural processes and human activities which are reducing the surface area covered by this key coastal ecosystem (Boudouresque *et al.*, 2006). The most important anthropogenic factors responsible for the decline of the seagrass are the decrease in water transparency (Ruiz and Romero, 2001), and the direct and indirect destruction of the meadows due to coastal development (Meinesz *et al.*, 1991), boat anchoring (Francour *et al.*, 1999; Milazzo *et al.*, 2004), trawling (González-Correa *et al.*, 2005), fish farming (Delgado *et al.*, 1997; Ruiz *et al.*, 2001), desalination plants (Latorre, 2005; Gacia *et al.*, 2007) and climate change (Peirano *et al.*, 2005). The beds under these pressures have a lower shoot density and a fragmented structure (Boudouresque *et al.*, 2006).

Disturbed *P. oceanica* beds seem to be more vulnerable and more easily colonised by introduced macrophytes (Occhipinti-Ambrogi and Savini, 2003). In the Mediterranean Sea, 85 macrophytes are introduced species, 9 of which are considered to be invasive, including the green alga *Caulerpa taxifolia* (Vahl) C. Agardh (Boudouresque and Verlaque, 2002). *Posidonia oceanica* has been found growing together with *C. taxifolia* for two decades. The alga is now found in 7 countries around the Mediterranean Sea (Meinesz *et al.*, 2001; Cevik *et al.*, 2007). In France, 8687 hectares of the sea floor were concerned by *C. taxifolia* (*sensu* Vaugelas *et al.*, 1999) at the end of 2005, with 88 zones of interactions with *P. oceanica* (Javel and Meinesz, 2006). Sparse *P. oceanica* beds are known to be more easily invaded by *C. taxifolia* than dense ones (Villèle and Verlaque, 1995). The biomass of *C. taxifolia* recorded inside shallow *P. oceanica* beds ranges from 6 to 12.5 kg w.wt.m⁻² (Verlaque and Fritayre, 1994; Villèle and Verlaque, 1995), which is much higher than the biomass recorded on rocks and muddy-sandy substrates (Thibaut *et al.*, 2004). In fact, *P. oceanica* has a positive effect on frond elongation of the alga in shallow waters (Ceccherelli and Cinelli, 1998). Interactions between the two macrophytes induce (i) an increase in phenol production by the seagrass (Villèle and Verlaque, 1995), (ii) a decrease in leaf length and longevity and (iii) an increase in the number of leaves produced each year (Dumay *et al.*, 2002). Although the ecological impact of *C. taxifolia* has been reported for several taxonomic groups (see Boudouresque *et al.*, 1995 for a review), all the observations recorded on *P. oceanica* were isolated or formed part of short-term experiments that did not

answer the key question: can *C. taxifolia* alter the structure of a *P. oceanica* bed? To this end we studied the competition between the two species over a 10-year period.

MATERIAL AND METHODS

Study sites

In order to compare the evolution and the structure of an invaded and a non-invaded *P. oceanica* bed, we assessed all the possible zones hosting similar *P. oceanica* beds (i.e. same depth, same hydrodynamic conditions and shoot density of the same order) situated along the French coast in 1995. Two sites were selected: Cap Martin with an invaded *P. oceanica* bed and Cap d'Antibes with a non-invaded bed.

The zone invaded by *C. taxifolia* is located at the tip of Cap Martin (Alpes Maritimes, France, 7°30'E 43°45'N), and the non-invaded seagrass bed is located at Cap d'Antibes (Alpes Maritimes, France, 7°07'E 43°33'N). Both sites are at 6 m depth and are frequently subjected to swell. Their *P. oceanica* shoot densities are qualified as normal (from 479 to 703 shoots m⁻²) according to the usual classification model used for *P. oceanica* study (Pergent *et al.*, 1995). *C. taxifolia* settled in 1995 in the invaded zone and was never observed at the reference site at Cap d'Antibes. Neither site suffers obvious human impact. In undisturbed beds, orthotropic shoots are more dominant than plagiotropic ones (Boudouresque *et al.*, 2006).

At each site (Cap Martin = invaded and Cap d'Antibes = non-invaded) a repeated-measures experimental design was set up with 20 permanent quadrats (25 x 25 cm²) randomly settled inside *P. oceanica* meadows. Each year, in July-August from 1995 to 2005 (except in 1996 and 1997), within each quadrat the percentage of substrate covered by *C. taxifolia* was estimated visually by means of a reticulated quadrat, and the shoot density and the number of orthotropic (vertical) and plagiotropic (horizontal) shoots was counted. The number of lateral branches less than 10 cm long (according to the terminology of Molenaar *et al.*, 2000) was counted to calculate the ramification ratio (number of branches/total number for shoots of each type of rhizome). These parameters are the most common ones used to describe impacts on the structure of *P. oceanica* beds (Pergent-Martini *et al.*, 2005).

Statistical analysis

In order to compare the influence of *C. taxifolia* on the mean shoot density and on the mean number of orthotropic and plagiotropic shoots of *P. oceanica*, and to assess temporal patterns, two-way repeated-measures ANOVAs were performed with sites (2 levels: invaded – control) and time (9 levels) as fixed factors, using the Geisser-Greenhouse approximation in order to avoid violation of the sphericity. When results of the different analysis were significant, the LSD a posteriori test was applied (Zar, 1999).

In order to test the relation between the influence of *C. taxifolia* and the time on the rate of ramifications, a chi-square test was performed.

RESULTS

Caulerpa taxifolia cover

At the start of the experiment at Cap Martin in 1995, the mean cover of *C. taxifolia* was 4%. Infestation increased rapidly to reach a maximum cover of 93% in 2000. A sharp decrease of *C. taxifolia* col-

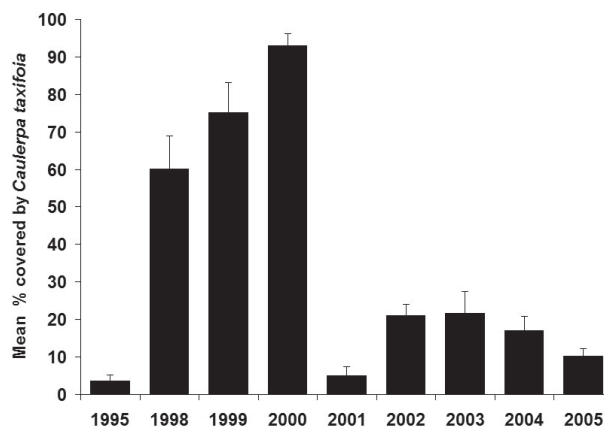


FIG. 1. – Mean cover of *Caulerpa taxifolia* (%), from 1995 to 2005, in the *Posidonia oceanica* meadow at Cap Martin. Error bars represent \pm SE.

onisation was observed within the quadrats in 2001 and the in following years the colonisation remained low, between 10 and 22% (Fig. 1).

Shoot density

The analysis of the influence of time on each site reflects a higher density of shoots of *P. oceanica* in 1995, 1998 and 1999 than in the following years,

TABLE 1. – 2-way Repeated-measures ANOVA using the Geisser-Greenhouse (G-G) approximation on the effects of the Site (invaded and non-invaded by *Caulerpa taxifolia*) and Time on the mean shoot density, the mean number of orthotropic shoots, and the mean number of plagiotropic shoots of *Posidonia oceanica*. LSD test - p value = 0.05.

	SS	d.f.	MS	F	p	G-G ϵ	G-G df1	G-G df2	p
Shoot density									
Intercept	30290194	1	30290194	451.78	<0.001				
Site	395462	1	395462	5.89	<0.05				
Error	1676155	25	67046						
Time	4322830	8	540354	20.19	<0.001	0.65	5.21	130.40	<0.001
Time*Site	2004343	8	250543	9.36	<0.001	0.65	5.21	130.40	<0.001
Error	5350226	200	26751						
LSD test: Invaded site = 1995=1998=1999>2000=2001=2002=2003=2004=2005 Control site = 1995=1998=1999>2000=2001=2002=2003=2004=2005									
Orthotropic shoots									
Intercept	23974758	1	23974758	505.47	<0.001				
Site	1575338	1	1575338	33.21	<0.001				
Error	1375470	29	47430						
Time	5835932	8	729491	34.89	<0.001	0.62	4.98	144.52	<0.001
Time*Site	3180318	8	397540	19.01	<0.001	0.62	4.98	144.52	<0.001
Error	4850233	232	20906						
LSD test: Invaded site = 1995=1998=1999>2000=2001=2002=2003=2004=2005 Control site = 1995=1998=1999>2000=2001=2002=2003=2004=2005									
Plagiotropic shoots									
Intercept	690125	1	690124.5	47.91	<0.001				
Site	179666	1	179665.8	12.47	<0.001				
Error	374501	26	14403.9						
Time	196577	8	24572.1	2.67	<0.01	0.43	3.49	90.78	<0.05
Time*Site	112974	8	14121.7	1.53	ns	0.43	3.49	90.78	ns
Error	1910396	208	9184.6						

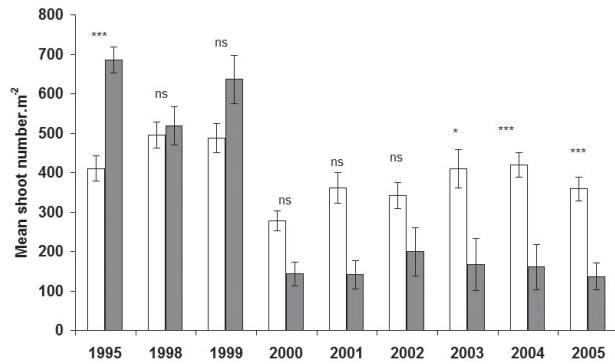


FIG. 2. – Mean shoot density of *Posidonia oceanica*, from 1995 to 2005, at the invaded site of Cap Martin (grey bars) and at the control site of Cap d’Antibes (white bars). Error bars represent \pm SE. Multiple comparison test invaded vs. control site year per year - LSD test: * $p<0.05$, ** $p<0.01$, *** $p<0.001$, ns non-significant.

whatever the level of invasion. A significant decrease in the shoot density occurred between 1999 and 2000 at both sites (from 636 to 143.2 shoots m^{-2} at the invaded site and from 488 to 277.6 at the control site) (LSD test $p<0.001$). When we studied the influence of time and invasion on the shoot density from 2000 to 2005, we found that the mean shoot densities remained similar from 2000 to 2002 at both sites. However, from 2003 to 2005 the mean shoot densities were lower (from 136 to 166.7 shoots m^{-2}) at the invaded site than at the control site (from 359 shoot m^{-2} to 419.2 shoot m^{-2}) (Fig. 2, Table 1).

Number of orthotropic and plagiotropic shoots

The evolution over time of the number of orthotropic shoots at the control site and invaded sites followed the same pattern as described for the density. The mean number of orthotropic shoots was similar from 1995 to 1999 but decreased in the following years. From 1999 to 2000, both sites showed a sharp decrease in the number of orthotropic shoots. In 2001 the mean number of orthotropic shoots was always greater and constant at the control site (from 271.2 to 477.6 shoot m^{-2}), whereas at the invaded site they completely disappeared in 2005 (Fig 3a, Table 1).

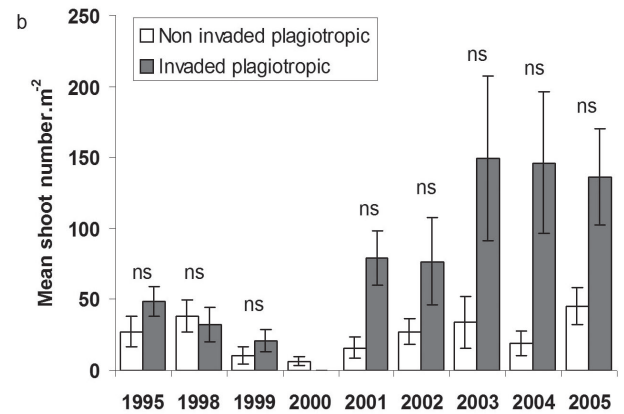
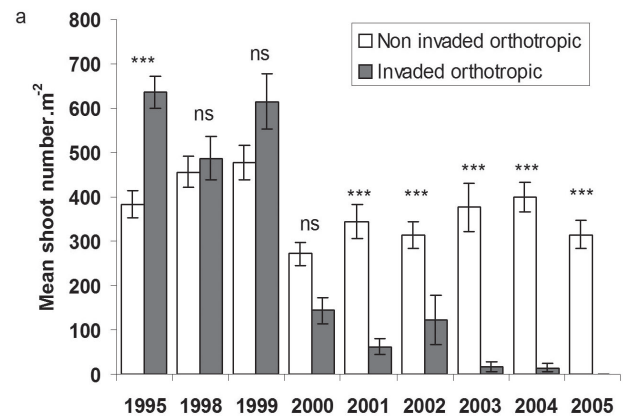


FIG. 3. – Mean number of orthotropic (a) and plagiotropic (b) shoots of *Posidonia oceanica*, from 1995 to 2005, at the control site of Cap d’Antibes (white bars) and the invaded site of Cap Martin (grey bars). Error bars represent \pm SE. Multiple comparison test invaded vs. control site year per year - LSD test: * $p<0.05$, ** $p<0.01$, *** $p<0.001$, ns = non-significant.

The evolution over time of the number of plagiotropic shoots at the control and invaded sites followed the same pattern from 1995 to 2000. In 2000, all the plagiotropic shoots at the invaded site had disappeared. Results of the site/time interaction (Table 1) show no statistical difference, whereas the mean number of plagiotropic shoots at the invaded site increased from 2001 to 2005 (Fig 3b, Table 1), which could be explained by a greater variability of the number of plagiotropic shoots within the quadrats.

TABLE 2. – Proportion (%) of the total number of ramifications measured on orthotropic (O) and plagiotropic (P) shoots / total number of orthotropic shoots of *Posidonia oceanica* measured at the invaded site by *Caulerpa taxifolia* of Cap Martin and at the non-invaded reference site of Cap d’Antibes from 1995 to 2005; - : absence of shoot.

	1995	1998	1999	2000	2001	2002	2003	2004	2005
O – non-invaded	8.14	16.64	3.52	5.31	18.56	8.28	22.15	4.40	13.96
O - invaded	9.94	3.45	2.34	0	3.85	1.31	0	0	-
P – non-invaded	50.00	50.00	61.54	50.00	60.00	59.12	50.00	62.50	67.86
P - invaded	40.98	40.00	65.38	-	54.55	66.67	34.82	24.18	48.24

Ramifications

The proportion of the ramifications at the control site ranged from 3.52 to 22.15% on orthotropic shoots, with higher values recorded in 1998, 2001, 2003 and 2005, and from 50 to 67.86% on plagiotropic shoots (Table 2).

At the invaded site, there were fewer ramifications on orthotropic shoots starting from 1998 and no more ramifications in 2000, 2003 and 2004 ($\chi^2_8 = 33.15$, $p < 0.000$). The proportion of ramifications on plagiotropic shoots ranged from 24.18 to 66.67%, with the lowest values recorded in 2003 and 2004 (Table 2).

DISCUSSION

In the year 2000, both studied *P. oceanica* beds suffered a decrease in their density; the causes are unknown but could be related to the episode of high temperatures in summer 1999 associated with mass mortality events of invertebrates (Cerrano *et al.*, 2000, Garrabou *et al.*, 2001, Linares *et al.*, 2005) and the impact on the growth of leaf and rhizome of deep plants of *P. oceanica* (Mayot *et al.*, 2005) observed in the western Mediterranean. The invasion of *C. taxifolia* on *P. oceanica* seemed to have increased this impact and did not allow the seagrass to recover its initial structure.

Within the 10 years of the study, *Posidonia oceanica* did not disappear within the permanent quadrats. However, we observed a drastic change in the structure of the meadow invaded by *C. taxifolia*. A significant decrease in shoot density was observed in 2000 when *C. taxifolia* reached its maximum infestation. The dense continuous bed of *P. oceanica* changed from a bed that was classified as having a 'normal' density to one with an 'abnormal' (i.e. more sparse) density according to the classification of Pergent *et al.* (1995). During the next 5 years the seagrass did not recover its initial density even after *C. taxifolia* decreased strongly.

Our study at the invaded site shows that the high biomass of *C. taxifolia* able to grow inside *P. oceanica* beds not only interacts physiologically with the plant (Cuny *et al.*, 1995; Villèle and Verlaque 1995; Dumay *et al.*, 2002) but can also change the structure of the invaded bed. The structural impact seems to be slow for several years between the beginning of the invasion and the record of the first changes in

the structure of the *P. oceanica* bed. Whereas non-invaded beds have a majority of orthotropic shoots, plagiotropic ones came to dominate in the invaded beds. This was particularly the case between 2000 and 2001, when the exclusively orthotropic shoots were transformed into plagiotropic ones. *Posidonia oceanica* reacts in the same way when beds are under anchoring stress, which leads to a higher proportion of plagiotropic shoots (Francour *et al.*, 1999; Milazzo *et al.*, 2004). This change denotes a colonisation phase of *P. oceanica* which is commonly observed after a stress event. Orthotropic shoots are transformed into plagiotropic shoots in order to recolonise the empty space.

Posidonia oceanica is not replaced by *C. taxifolia* even ten years after invasion. It has been suggested that the seagrass acts as a barrier against *C. taxifolia* (Thibaut, 2001). *Posidonia oceanica* has a contrasting effect on the growth and survival of *C. taxifolia* (Ceccherelli and Cinelli, 1998, 1999) and infestation of dense *P. oceanica* meadows is possible but not frequent (Thibaut, 2001). When *C. taxifolia* settles inside dense *P. oceanica* beds, its biomass reaches maximum values, leading to sedimentation inside the bed, and thus creates an anoxic substrate (Finzer and Poizat, 1996). We can hypothesise that the combination of the chemical interaction and the over-sedimentation could be responsible for the change in the *P. oceanica* structure in our study area. The decrease of *P. oceanica* shoot density could favour a rapid recolonisation by *C. taxifolia* in the quadrats. However the percentage of infestation by the algae within the quadrat remained constant at around 10-22%, which could be explained by the fact that the plagiotropic shoots, which have mostly replaced the orthotropic ones, have a negative effect on *C. taxifolia* growth and expansion, as observed on the seagrass boundaries where rhizome movements scour the algae (Ceccherelli *et al.*, 1999; Thibaut, 2001).

At a Mediterranean scale, *C. taxifolia* has been continuously expanding since it was found in 1984 (Meinesz and Hesse 1991; Javel and Meinesz, 2006), although local regressions of *C. taxifolia* in previously highly invaded zones have already been observed. In the port of Villefranche-sur-Mer, *C. taxifolia* colonisation decreased sharply in 1999 along with a bloom of Sacoglossan herbivores (Thibaut and Meinesz, 2000). In the port of St-Cyprien (Pyrénées-Orientales, western France) *C. taxifolia* disappeared completely in 2002. Cap Martin is the first location in the open sea where a massive regression was ob-

served (Levi, 2004). The cause of these regressions remains unknown. The only common factor of them all is that *C. taxifolia* has been colonising these areas for years and that the substrates have been heavily colonised (Javel and Meinesz, 2006) with a maximum of algal biomass (Thibaut *et al.*, 2004). The influence of a warm event does not seem to have affected *C. taxifolia* directly, though it performs better in warm conditions (Komatsu *et al.*, 1997). A cold temperature episode could have been responsible for the massive regression recorded in 2001. A similar regression event also occurred in the northern Adriatic in 2000-2001 after 6 years of infestation, but low temperature was not the cause (Ivesa *et al.*, 2006).

It seems that small quantities of *C. taxifolia* within *P. oceanica* still allow the recovery of the empty space by plagiotropic rhizomes. If *C. taxifolia* infestation remains low, recovery by plagiotropic shoots is possible but will take several years, as observed in stressed meadows (González-Correa *et al.*, 2005), due to the slow growth of the horizontal rhizomes (0.4-7.4 cm year⁻¹; Boudouresque and Jeudy de Grissac, 1983). Globally, changes in the beds are a long process and longer-term studies are needed to follow the ecological impact of *C. taxifolia* in the Mediterranean.

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