

# Experimental removal of the invasive *Caulerpa racemosa* triggers partial assemblage recovery

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*The invasive species Caulerpa racemosa var. cylindracea represents a serious threat to the diversity of benthic assemblages in the Mediterranean Sea. In the present study, a removal experiment was carried out to test whether, after 18 months of C. racemosa var. cylindracea exclusion, the macrophyte assemblage resembled a non-invaded assemblage. The results show that in the assemblage invaded by C. racemosa var. cylindracea the number of species, macrophyte cover, Shannon diversity and Pielou's evenness were lower than in the non-invaded assemblage. Erect perennial species were particularly affected and other introduced species were significantly reduced or completely excluded. After 18 months of removal/exclusion of C. racemosa var. cylindracea, only partial recovery of the macrophyte assemblage could be observed. Species numbers, total cover and erect perennial species cover were still significantly lower than in the non-invaded plots. However Shannon diversity and Pielou's evenness had reached comparable levels. In contrast to native macrophytes, the total cover of other introduced species reached a level comparable to the non-invaded plots. In summary, the present study revealed that after 18 months of C. racemosa var. cylindracea exclusion: (i) only partial recovery of the macrophyte assemblage occurred; and (ii) the development of other invasive species was favoured by the absence of C. racemosa var. cylindracea (Sisyphus effect).*

**Keywords:** biological invasions, dead *Posidonia oceanica* 'matte', invasion impact, marine macrophytes, Mediterranean Sea, species introductions

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## INTRODUCTION

The preservation of species and the restoration of natural habitats are urgently needed measures to fight against species and habitat degradation caused by anthropogenic impacts. Invasive species have played a major role in global change and biodiversity loss in the 20th Century and early 21st Century (Soulé, 1990; Gray, 1997; Vitousek *et al.*, 1997; Sala *et al.*, 2000). Invasive species are capable of changing species composition, abundance and diversity, thereby profoundly altering host ecosystems. At a more general level, invasive species are capable of changing important ecosystem functions such as nutrient cycling and primary productivity, hydrology, disturbance regimes and trophic structures. In all cases, the phenomenon of species introductions represents an irreversible ecosystem change (Vitousek *et al.*, 1997). Invasive species are characterized by a high capacity for spread and a negative ecological and/or economic impact (Alpert *et al.*, 2000; Boudouresque & Verlaque, 2002).

Apart from the abundant literature on descriptive studies of invasion impacts, there is a considerable lack of manipulative experimental evidence (Levine *et al.*, 2003; Hulme &

Bremner, 2006). In order to assess the impact of an invasive species, invaded assemblages are commonly compared to non-invaded ones (Levine *et al.*, 2003). However, due to the characteristics of invasive species that tend to monopolize large extents of substrate (Alpert *et al.*, 2000; Richardson *et al.*, 2000; Boudouresque & Verlaque, 2002), it is difficult to find non-invaded and invaded assemblages in the same study site and often the two assemblages are situated in different sites. Consequently, invasive species removal or addition may be an interesting trail to follow (Zavaleta *et al.*, 2001).

Invasive species removal is also performed in the frame of eradication and control campaigns in order to restore the native flora and fauna (Myers *et al.*, 2000; Zavaleta *et al.*, 2001; Simberloff *et al.*, 2005). After removal of the invasive species the system is assumed to return to its state before invasion. In the case of a plant assemblage, the recovery is influenced by propagule pressure which itself is dependent on: (1) presence of a seed bank; (2) distance to propagule sources; and (3) propagule availability (period of the year and seasonal cycles of species). Thus the time for an assemblage to recover to its non-invaded state may greatly vary.

Due to its geographical position at the intersection between the Atlantic and Indo-Pacific Oceans, the opening of the Suez Canal, intensive aquaculture and maritime traffic, the Mediterranean Sea is a worldwide hotspot of marine macrophyte introductions (Ribera Siguan, 2003; Boudouresque & Verlaque, 2005). Nearly 600 plant and animal species,

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representing 5% of the known flora and fauna, are estimated to have been introduced into the Mediterranean Sea (Boudouresque & Verlaque, 2005; Boudouresque *et al.*, 2005; Zenetos *et al.*, 2005). Since 1990, the introduced *Caulerpa racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman & Boudouresque (hereafter *Caulerpa racemosa*) has invaded the coasts of 12 Mediterranean countries at an almost unprecedented rate of spread (Verlaque *et al.*, 2000, 2004; Piazzini *et al.*, 2005; Klein & Verlaque, 2008). With its high rate of spread—colonization of nearly the entire Mediterranean Sea within 17 years—and its capability to alter benthic assemblages, *Caulerpa racemosa* may be considered as one of the most problematic invasive species in the Mediterranean Sea (Klein & Verlaque, 2008).

Different approaches have been explored to investigate the invasion impact of this Australian species in the Mediterranean Sea. Several studies have attempted to evaluate the impact by comparing the flora and fauna associated with *Caulerpa racemosa* meadows to other Mediterranean rhizophytic macrophytes, such as the native *Caulerpa prolifera* (Forsskål) J.V. Lamouroux and seagrasses (Di Martino & Giaccone, 1996; Buia *et al.*, 2001). Yet, the largest part of *C. racemosa* impact studies has dealt with comparisons between *C. racemosa* meadows and non-invaded *Posidonia oceanica* (Linnaeus) Delile dead 'matte' or hard substrata (rock and coralligenous assemblages) (Piazzini *et al.*, 2001, 2003, 2005, 2007; Carriglio *et al.*, 2003; Balata *et al.*, 2004; Casu *et al.*, 2005; Klein & Verlaque, 2009a, b).

The aim of the present study was to experimentally test the effect of *C. racemosa* on Mediterranean macrophyte assemblages. Therefore, a manual removal experiment has been carried out over a period of 18 months. A comparison was made between three macrophyte assemblages on dead *Posidonia oceanica* 'matte': (1) an assemblage invaded by *C. racemosa* (Invaded); (2) an assemblage where *C. racemosa* has been removed and excluded for 18 months (Removed); and (3) a non-invaded assemblage (Non-invaded).

## MATERIALS AND METHODS

### Area description

The present study was carried out in the bay of Marseilles (France, north-west Mediterranean Sea) ( $43^{\circ}13'44''\text{N}$   $5^{\circ}20'41''\text{E}$ ) where *Caulerpa racemosa* has been present since 1997 (Jousson *et al.*, 1998). *Caulerpa racemosa* forms meadows exhibiting a marked seasonal development pattern with a maximum in late summer with 100% cover and highest biomass (September 2002:  $82 \pm 3 \text{ g DW m}^{-2}$ ) and a minimum in winter (Ruitton *et al.*, 2005).

### Experimental procedures

Three different assemblages were considered: Invaded, Removed and Control. All assemblages were situated at 17 m depth on dead *Posidonia oceanica* 'matte'<sup>1</sup>.

<sup>1</sup>Dead 'matte': underlying structure of *Posidonia oceanica* meadows constituted of rhizomes and roots intermingled with sediments. This structure becomes apparent after the death of the seagrass and constitutes a particular habitat in the Mediterranean Sea.

For the Removed assemblage, *Caulerpa racemosa* was removed in August 2003 from five randomly positioned 20 cm × 20 cm plots. This manual removal was carried out very delicately, by pulling out all small fragments visible to the naked eye within the plot and in a margin around the plots without removing the other macrophytes. Then *C. racemosa* was excluded for 18 months until March 2005. In March 2005, the five Removed plots and five randomly positioned 20 cm × 20 cm plots were sampled both in the Invaded and the Control assemblages. Sampling was carried out by SCUBA diving. Samples were preserved in 4% formaldehyde–seawater until further treatment.

As a consequence of the miniaturization of the Mediterranean flora, the qualitative minimum sampling area is very small compared to other regions of the world (Coppejans, 1980). This area was determined for various subtidal and intertidal Mediterranean macrophyte assemblages and was always found to be comprised between 64 cm<sup>2</sup> and 200 cm<sup>2</sup> (Boudouresque, 1974; Cinelli *et al.*, 1977a, 1977b; Boudouresque & Belsher, 1979a, 1979b; Coppejans, 1980). The size of the sampling plots used in the present study was fixed at 400 cm<sup>2</sup> (20 cm × 20 cm) which is largely representative.

Eighteen months of removal/exclusion have been chosen, because a preliminary experimental study on the macrophyte assemblages on dead *Posidonia oceanica* 'matte' of the Port-Cros National Park showed recovery after complete destruction within 12 months (P. Helman, personal communication).

### Sample analysis

An exhaustive macrophyte species list (Chlorophyta, Ochrophyta (Heterokontophyta), Rhodophyta) was drawn up for each plot, by analysing the entire sample under a binocular microscope and light microscope. For all species the taxonomic nomenclature of the database *AlgaeBase* (Guiry & Guiry, 2009) was used. Introduced species were identified using the checklists of Boudouresque & Verlaque (2002) and Wallentinus (2002). Cover was measured for each species, by spreading out the thalli and measuring the surface covered (Boudouresque, 1971; Ballesteros, 1984). The dry weight of *Caulerpa racemosa* and other macrophytes was quantified for each plot by drying the macrophytes in an oven at 60°C until constant weight. Each macrophyte species was classified in one of the following functional form groups (Littler & Littler, 1980; Steneck & Dethier, 1994): articulated calcareous (= jointed calcareous), encrusting, epiphytes (very small microscopic epiphytes < 1 mm high), filamentous (filamentous and thin sheets/foliose) and erect (more complex structure or bigger than filamentous).

### Data analysis

Normality of data was evaluated using the Kolmogorov–Smirnov test. If data were normally distributed, a test of homogeneity of variances (Bartlett's test) and a 1-way ANOVA were carried out. Significant differences between assemblages were detected by the Student–Newman–Keuls (SNK) test. An analysis of similarities (ANOSIM) was carried out on the similarity matrix (Bray–Curtis similarity) calculated from macrophyte species cover for each sample. A non-metric multidimensional scaling (nMDS) plot was constructed using

as input data macrophyte species cover (including *Caulerpa racemosa*) for each sample.

For the ANOSIM and the nMDS plot the program Primer 6 has been used and the program Statistica 6.1 StatSoft® was used for all other statistical analyses.

## RESULTS

### *Caulerpa racemosa* cover and biomass

In the Non-invaded assemblage, *Caulerpa racemosa* was found with insignificant cover (0.88% of the cover of the plots) and biomass (Figure 1). In the Removed assemblage, during the 18 months of the experiment re-growth by creeping axes originating from the adjacent meadows was occasionally observed only in the margins around the plots. Moreover, few tiny fragments were occasionally found inside the plots. They may originate from microscopic *C. racemosa* filaments remaining in the 'matte' after removal, propagules or sexual reproduction from the surrounding meadows. Finally, in the Invaded assemblage, biomass of *C. racemosa* was  $1.27 \pm 0.22$  g DW plot<sup>-1</sup> (Figure 1) corresponding to a mean cover of  $133.20 \pm 25.89$  cm<sup>2</sup> plot<sup>-1</sup> (mean  $\pm$  SE), which represented up to 90% of the total macrophyte cover.

### Species richness, cover and biomass

Overall 124 taxa were identified, among them 85 Rhodophyta, 24 Chlorophyta and 15 Ochrophyta (Appendix). For the Non-invaded assemblage, significantly highest number of species (mean  $\pm$  SE:  $72 \pm 2$  species per plot;  $P < 0.001$ ) and highest macrophyte biomass ( $1.42 \pm 0.02$  g DW plot<sup>-1</sup>;  $P < 0.001$ ) (Figure 2A & B) were recorded. The highest value for the Shannon diversity index ( $H' = 4.89$ ) and high Pielou's evenness (mean =  $0.62 \pm 0.07$ ) were found in samples of the Non-invaded assemblage (Table 1). Chlorophyta and Rhodophyta dominated (Table 2) and the erect perennial species *Flabellia petiolata* (Turra) Nizamuddin represented the major component.

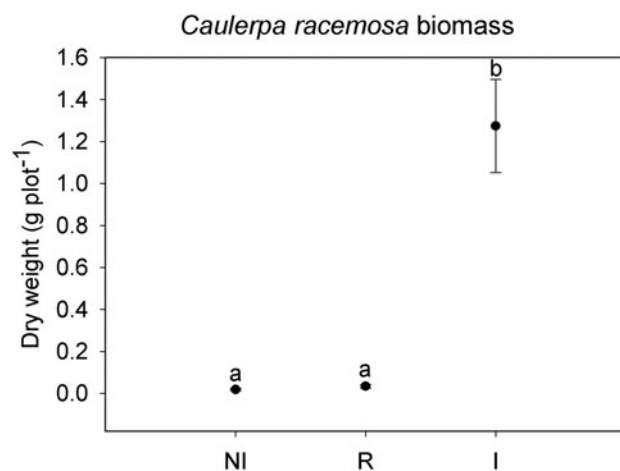


Fig. 1. *Caulerpa racemosa* dry weight (g DW plot<sup>-1</sup>) (mean  $\pm$  SE) in March 2005. NI, Non-invaded; R, Removed; I, Invaded. Values not different at  $\alpha = 5\%$  are denoted with the same letter (Student–Newman–Keuls test).

Of all assemblages, the lowest number of species ( $53 \pm 3$  species per plot), significantly lowest macrophyte biomass ( $0.20 \pm 0.07$  g DW plot<sup>-1</sup>;  $P < 0.001$ ) (Figure 2A & B), the lowest values for  $H'$  (maximum 1.85) and significantly lowest evenness ( $0.21 \pm 0.03$ ;  $P < 0.001$ ) (Table 1) were found in the Invaded assemblage. No dominant algal phylum could be discerned. Compared to the Non-invaded assemblage, the abundance of erect and filamentous species was strongly reduced (Table 2) and a number of species were completely excluded (Appendix) in the Invaded assemblage. The other introduced species significantly decreased in cover ( $P = 0.01$ ) (particularly 'Falkenbergia rufolanosa' (Harvey) F. Schmitz' phase and *Womersleyella setacea* (Hollenberg) R.E. Norris) and several species were completely lacking (*Acrothamnion preissii* (Sonder) E.M. Wollaston, *Antithamnion amphigeneum* A.J.K. Millar and *Asparagopsis armata* Harvey) (Figure 3).

In the Removed assemblage, species richness remained significantly lower than in the Non-invaded assemblage (SNK test:  $P < 0.01$ ) without a significant increase compared to the Invaded assemblage ( $60 \pm 2$  species per plot) (Figure 2A). On the other hand, macrophyte biomass significantly increased while still remaining lower than in the

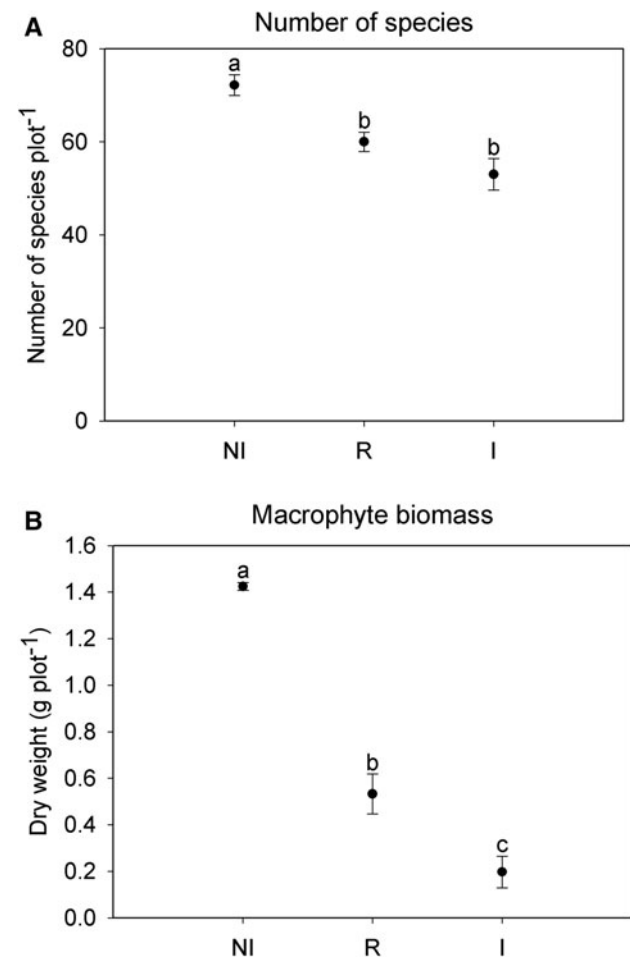


Fig. 2. (A) Macrophyte species number and (B) dry weight (g DW plot<sup>-1</sup>) excluding *Caulerpa racemosa* (mean  $\pm$  SE). NI, Non-invaded; R, Removed; I, Invaded. Values not different at  $\alpha = 5\%$  are denoted with the same letter (Student–Newman–Keuls test).

**Table 1.** Shannon diversity and evenness indices of the Non-invaded (NI), Removed (R) and Invaded (I) assemblage.

	Shannon index		Evenness	
	Minimum	Maximum	Mean	SE
NI	2.34	4.89	0.62	0.07
R	3.40	4.55	0.67	0.03
I	0.93	1.85	0.21	0.03

Non-invaded assemblage ( $0.53 \pm 0.09$  g DW plot<sup>-1</sup>; SNK test R-I:  $P < 0.05$ ; R-NI:  $P < 0.01$ ) (Figure 2B). The filamentous group clearly dominated whereas perennial erect species had not yet recovered (Table 2). No recruitment of the perennial erect species *Flabellia petiolata* occurred, a species which dominated in the Non-invaded assemblage. Rhodophyta dominated in terms of number of species and cover (Table 2). In contrast to native macrophytes, the total cover of other introduced species reached a level comparable to the Non-invaded assemblage (Figure 3).

The ANOSIM carried out pairwise on the three assemblages, with species cover (including *C. racemosa*) as input data, showed high R values for the Non-invaded and Invaded (0.992), Removed and Invaded assemblages (0.996) and lower values for the Non-invaded and Removed assemblages (0.352). These results suggest that in the Invaded assemblage the number of species and their cover were different from the other two. The Non-invaded and the Removed assemblages showed more similarity.

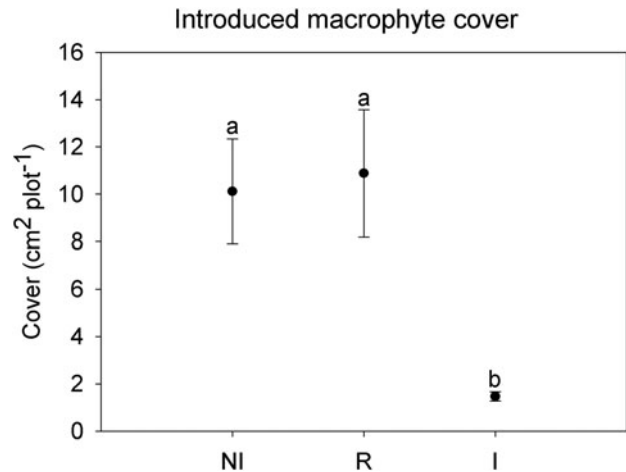
The nMDS plot showed a clear opposition of the Invaded assemblage dominated by *C. racemosa* at one end and Removed and Non-invaded assemblages at the other end (Figure 4). Inside the cluster of Non-invaded and Removed assemblages a change can be seen from a Non-invaded assemblage associated with the perennial species *Flabellia petiolata*, *Codium bursa* (Olivi) C. Agardh and *Phyllophora sicula* (Kützinger) Guiry & L.M. Irvine to the Removed assemblage associated with the filamentous species *Womersleyella setacea* and *Cladophora laetevirens* (Dillwyn) Kützinger.

## DISCUSSION

In the Mediterranean Sea the invasive *Caulerpa racemosa* mainly colonizes dead *Posidonia oceanica* 'matte' and deep detritic assemblages (Klein & Verlaque, 2008, 2009a). Furthermore, *C. racemosa* is commonly found in urbanized areas near large cities and ports (Athens, Genoa, Livorno, Taranto, Toulon, etc) (Klein & Verlaque, 2008). Therefore, the bay of Marseilles can be considered as representative of many other invaded areas in the Mediterranean Sea.

**Table 2.** Cover (cm<sup>2</sup> plot<sup>-1</sup>) of the different macrophyte phyla and functional form groups of the Non-invaded (NI), Removed (R) and Invaded (I) assemblage (mean  $\pm$  SE).

	Macrophyte phyla			Functional form groups				
	Chlorophyta	Ochrophyta	Rhodophyta	Articulated calcareous	Encrusting	Epiphytes	Erect	Filamentous
NI	25.22 ( $\pm 10.04$ )	4.76 ( $\pm 0.53$ )	24.69 ( $\pm 4.15$ )	0.18 ( $\pm 0.15$ )	0.24 ( $\pm 0.16$ )	0.61 ( $\pm 0.01$ )	31.14 ( $\pm 10.23$ )	22.49 ( $\pm 3.90$ )
R	4.28 ( $\pm 1.26$ )	4.49 ( $\pm 0.79$ )	24.67 ( $\pm 5.45$ )	0.66 ( $\pm 0.36$ )	0.04 ( $\pm 0.04$ )	0.58 ( $\pm 0.01$ )	8.25 ( $\pm 1.76$ )	23.91 ( $\pm 4.51$ )
I	7.96 ( $\pm 1.11$ )	4.08 ( $\pm 1.82$ )	9.04 ( $\pm 1.42$ )	0.42 ( $\pm 0.24$ )	0.01 ( $\pm 0.01$ )	0.54 ( $\pm 0.01$ )	8.67 ( $\pm 1.50$ )	11.44 ( $\pm 1.37$ )

**Fig. 3.** Introduced species cover (cm<sup>2</sup> plot<sup>-1</sup>) excluding *Caulerpa racemosa* (mean  $\pm$  SE). NI, Non-invaded; R, Removed; I, Invaded. Values not different at  $\alpha = 5\%$  are denoted with the same letter (Student–Newman–Keuls test).

## Non-invaded dead 'matte' assemblage

At Marseilles, in the Non-invaded assemblage, the macrophyte assemblage on dead *Posidonia oceanica* 'matte' were similar to the macrophyte assemblages studied in Italy and south-eastern France (Augier & Boudouresque, 1967; Cinelli & Salghetti-Drioli, 1983–1984; Salghetti-Drioli *et al.*, 1985, 1989; Piazzini *et al.*, 2001). The samples were typical of the cold season in the north-western Mediterranean Sea with the dominance of Rhodophyta and Chlorophyta. In contrast with previous studies, species richness was high, and species composition differed with regard to the dominant species, probably due to greater depth and colder annual temperatures. The nearly absence of articulated calcareous and encrusting species was a general feature common to all the samples.

## *Caulerpa racemosa* invasion impact

In contrast with previous years, when *Caulerpa racemosa* showed a seasonal development with a temporal complete withdrawal in winter (Ruitton *et al.*, 2005) an important *C. racemosa* cover was present in March 2005. This tendency of *C. racemosa* to becoming a permanent part of the macrophyte assemblage in the bay of Marseilles has been confirmed in subsequent years (2006 and 2007; personal observation), indicating a possible acclimation to local conditions. The *C. racemosa* biomass was comparable to the biomass found during the same season in the warmer region of the French Riviera (Villefranche-sur-mer) (Capiomont *et al.*, 2005).

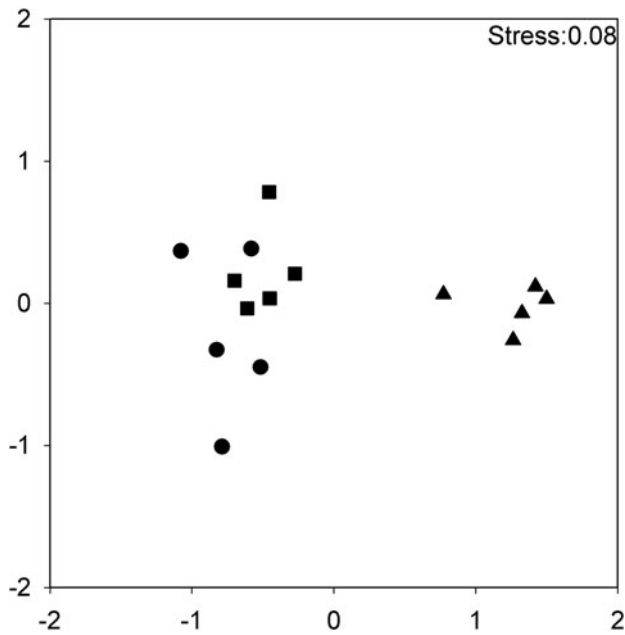


Fig. 4. Non-metric multidimensional scaling plot of the macrophyte assemblage in the Non-invaded (●), Removed (■) and Invaded assemblage (▲).

The negative effects caused by the invasion by *C. racemosa* observed in the present study were consistent with previous descriptive studies conducted in Italy and the bay of Marseilles (France). Macrophyte assemblages of dead *Posidonia oceanica* 'matte' showed reduced species number and abundance in the presence of *C. racemosa* (Piazzi *et al.*, 2001; Piazzi & Cinelli, 2003; Balata *et al.*, 2004; Klein & Verlaque, 2009b). Although *C. racemosa* biomass was more than five times lower at Marseilles than in Italy (Piazzi *et al.*, 2001), it is important to notice that the invasion effect was equally drastic.

Decreased species diversity through competitive exclusion is a widespread effect of invasive species (Morrison, 2000; Brown *et al.*, 2002; Branch & Steffani, 2004; Bando, 2006). Thus the decrease in macrophyte species numbers and abundance in the assemblage invaded by *C. racemosa* may be explained by *C. racemosa*'s competitive superiority. *Caulerpa racemosa* is also known to contain various secondary metabolites that are supposed to play a role in herbivore deterrence and may be in competition (Klein & Verlaque, 2008).

In the Invaded assemblage, the reduction in biomass ('*Falkenbergia rufolanosa*' phase, *Womersleyella setacea*) or absence (*Acrothamnion preissii*, *Antithamnion amphigenum* and *Asparagopsis armata*) of other introduced species found in the Non-invaded assemblage suggests that *C. racemosa* was competitively superior not only to the native species but also to the other introduced macrophytes present in the bay of Marseilles. Similar results have been found in Italy, where the abundance of the invasive species *Womersleyella setacea* was reduced in the presence of *C. racemosa* (Piazzi & Cinelli, 2003).

### Effect of *Caulerpa racemosa* removal

After 18 months of manually removing and excluding *Caulerpa racemosa*, the macrophyte assemblage of dead

*P. oceanica* 'matte' was still significantly different from the Non-invaded assemblage, indicating that this time period was not long enough.

A similar study of removal was carried out by Piazzi & Ceccherelli (2006) over one year on rocky substrate. The results showed that in the Invaded assemblage, the erect and filamentous group was little affected by *C. racemosa* in contrast to the encrusting functional form group that was eliminated. After one year of removal, the erect and filamentous group recovered completely, whereas no sign of recovery was detected for the encrusting group and the levels of the Non-invaded assemblage had not been reached in terms of percentage cover and species number.

In the Removed plots of the present study, the development of other invasive species was more facilitated by the removal of *C. racemosa* than Mediterranean species. This may have important consequences for the subsequent development of the assemblage. Similar results have been found in some cases in terrestrial and fresh water environments where increased abundance of other introduced species was observed after removal or control of certain invasive species, a phenomenon called the Sisyphus-effect (Mack & Lonsdale, 2002).

On the one hand, the relatively high species richness and partial recovery of the assemblage observed in the Removed plots showed the development potential of the macrophyte assemblage after removal of *C. racemosa*. On the other hand, the removal favoured first the development of other invasive species, in particular the filamentous Rhodophyta *Womersleyella setacea*, which recovered faster than the native species and become dominant in the assemblage.

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**Appendix.** Presence (+) and absence (–) of each macrophyte species in the Non-invaded, Removed and Invaded assemblage. Phyla: C, Chlorophyta; O, Ochrophyta; R, Rhodophyta.

	Phylum	Non-Invaded	Removed	Invaded
<i>Acetabularia acetabulum</i> (Linnaeus) P.C. Silva	C	–	–	+
<i>Acinetospora crinita</i> (Carmichael) Kornmann	O	+	–	–
<i>Acrochaete inflata</i> (Ercegovic) Gallardo <i>et al.</i>	C	+	+	+
<i>Acrochaetium</i> sp.	R	+	+	+
<i>Acrosorium ciliolatum</i> (Harvey) Kylin	R	+	+	+
<i>Acrothamnion preissii</i> (Sonder) E.M. Wollaston	R	+	–	–
<i>Aglaothamnion gallicum</i> (Nägeli) L'Hardy-Halos & Ardré	R	+	+	+
<i>Aglaothamnion tenuissimum</i> (Bonnemaison) Feldmann-Mazoyer	R	+	+	+
<i>Aglaothamnion tripinnatum</i> (C. Agardh) Feldmann-Mazoyer	R	+	+	–
<i>Anotrichium barbatum</i> (C. Agardh) Nägeli	R	+	+	+
<i>Antithamnion amphigeneum</i> A.J.K. Millar	R	+	+	–
<i>Antithamnion cruciatum</i> (C. Agardh) Nägeli	R	+	+	+
<i>Antithamnion heterocladum</i> Funk	R	+	+	–
<i>Antithamnion tenuissimum</i> (Hauck) Schiffner	R	+	+	+
<i>Apoglossum ruscifolium</i> (Turner) J. Agardh	R	+	–	–
<i>Ascocyclus orbicularis</i> (J. Agardh) Kjellman	O	–	–	+
<i>Asparagopsis armata</i> Harvey	R	+	+	–
<i>Bryopsis feldmannii</i> Gallardo & G. Furnari	C	+	+	+
<i>Bryopsis monoica</i> Berthold ex Funk	C	–	–	+
<i>Caulerpa racemosa</i> var. <i>cylindracea</i> (Sonder) Verlaque, Huisman & Boudouresque	C	+	+	+
<i>Ceramium ciliatum</i> (J. Ellis) Ducluzeau	R	+	+	+
<i>Ceramium cimbricum</i> H.E. Petersen	R	+	–	–
<i>Ceramium diaphanum</i> (Lightfoot) Roth	R	–	–	+
<i>Ceramium echionotum</i> J. Agardh	R	+	+	+
<i>Ceramium flaccidum</i> (Kützing) Ardissonne	R	+	+	+
<i>Ceramium giacconeii</i> Cormaci & G. Furnari	R	+	+	–
<i>Ceramium secundatum</i> Lyngbye	R	+	+	–
<i>Ceramium strictum</i> sensu Harvey	R	+	+	+
<i>Chaetomorpha aerea</i> (Dillwyn) Kützing	C	+	+	+
<i>Champia parvula</i> (C. Agardh) Harvey	R	+	+	+
<i>Chondria capillaris</i> (Hudson) M.J. Wynne	R	+	+	+
<i>Chondria dasyphylla</i> (Woodward) C. Agardh	R	+	+	+
<i>Choristocarpus tenellus</i> Zanardini	O	+	+	+
<i>Chroodactylon ornatum</i> (C. Agardh) Basson	R	+	–	–
<i>Chylocladia verticillata</i> (Lightfoot) Bliding	R	+	–	–
<i>Cladophora albida</i> (Nees) Kützing	C	+	–	–
<i>Cladophora coelothrix</i> Kützing	C	+	–	–
<i>Cladophora dalmatica</i> Kützing	C	+	–	–
<i>Cladophora echinus</i> (Biasoletto) Kützing	C	–	–	+
<i>Cladophora laetevirens</i> (Dillwyn) Kützing	C	+	+	+
<i>Cladophora lehmanniana</i> (Lindenberg) Kützing	C	–	+	+
<i>Cladophora prolifera</i> (Roth) Kützing	C	+	+	+
<i>Cladophora rupestris</i> (Linnaeus) Kützing	C	+	+	+
<i>Cladophora sericea</i> (Hudson) Kützing	C	–	+	+
<i>Cladostephus spongiosus</i> f. <i>verticillatus</i> (Lightfoot) Prud'homme van Reine	O	–	+	–
<i>Codium bursa</i> (Linnaeus) C. Agardh	C	+	+	+
<i>Codium vermilara</i> (Olivi) Delle Chiaje	C	–	+	–
<i>Compsothamnion thuyoides</i> (J.E. Smith) Nägeli	R	+	+	+
<i>Corallina elongata</i> J. Ellis & Solander	R	–	+	+
<i>Cordylecladia guiryi</i> Gargiulo, G. Furnari & Cormaci	R	+	–	–
<i>Crouania attenuata</i> (C. Agardh) J. Agardh	R	+	+	+
<i>Dasya corymbifera</i> J. Agardh	R	+	+	+
<i>Dasya ocellata</i> (Grateloup) Harvey	R	+	+	–
<i>Dasya rigidula</i> (Kützing) Ardissonne	R	+	–	–
<i>Dasyella gracilis</i> Falkenberg	R	+	–	–
<i>Dictyopteris polypodioides</i> (A.P. de Candolle) J.V. Lamouroux	O	+	+	+
<i>Dictyota dichotoma</i> (Hudson) J.V. Lamouroux	O	+	+	+
<i>Entocladia viridis</i> Reinke	C	+	+	–
<i>Erythrotrichia carnea</i> (Dillwyn) J. Agardh	R	+	+	+
<i>Erythrotrichia simplex</i> P. Dangeard	R	+	+	+
<i>Falkenbergia rufolanosa</i> (Harvey) F. Schmitz' phase of <i>Asparagopsis armata</i>	R	+	+	+
<i>Feldmannophycus rayssiae</i> (Feldmann & G. Feldmann) Augier & Boudouresque	R	+	+	+
<i>Flabellia petiolata</i> (Turra) Nizamuddin	C	+	+	+

Continued



## Appendix. Continued

	Phylum	Non-Invaded	Removed	Invaded
<i>Gelidium</i> sp.	R	-	-	+
<i>Halarachnion ligulatum</i> (Woodward) Kützing	R	+	+	-
<i>Halodictyon mirabile</i> Zanardini	R	+	-	-
<i>Halopteris filicina</i> (Grateloup) Kützing	O	+	+	+
<i>Haraldia lenormandii</i> (Derbès & Solier) Feldmann	R	+	+	+
<i>Herposiphonia secunda</i> (C. Agardh) Ambronn	R	+	+	+
<i>Herposiphonia secunda</i> f. <i>tenella</i> (C. Agardh) M.J. Wynne	R	+	+	+
<i>Heterosiphonia crispella</i> (C. Agardh) M.J. Wynne	R	+	+	+
<i>Hinckia sandriana</i> (Zanardini) P.C. Silva	O	+	-	+
<i>Hydrolithon farinosum</i> (J.V. Lamouroux) D. Penrose & Y.M. Chamberlain	R	-	+	-
<i>Jania rubens</i> var. <i>corniculata</i> (Linnaeus) Yendo	R	+	+	+
<i>Kallymenia patens</i> (J. Agardh) Parkinson	R	+	-	-
<i>Kuckuckia spinosa</i> (Kützing) Kornmann	O	-	+	-
<i>Laurencia microcladia</i> Kützing	R	+	+	+
<i>Lomentaria chylocladiella</i> Funk	R	+	+	+
<i>Lomentaria ercegovicii</i> Verlaque, Boudouresque, Meinesz, Giraud & Marcot Coqueugniot	R	+	-	+
<i>Lomentaria verticillata</i> Funk	R	+	+	+
<i>Monosporus pedicellatus</i> (J.E. Smith) Solier	R	+	+	+
<i>Myrionema strangulans</i> Greville	O	+	+	+
<i>Nitophyllum punctatum</i> (Stackhouse) Greville	R	+	-	+
<i>Peyssonnelia rosa-marina</i> Boudouresque & Denizot	R	-	-	+
<i>Peyssonnelia rubra</i> (Greville) J. Agardh	R	+	+	-
<i>Phyllophora sicula</i> (Kützing) Guiry & L.M. Irvine	R	+	+	+
<i>Pleonosporium borneri</i> (J.E. Smith) Nägeli	R	+	+	+
<i>Plocamium cartilagineum</i> (Linnaeus) P.S. Dixon	R	+	+	+
<i>Pneophyllum confervicola</i> (Kützing) Y.M. Chamberlain	R	+	+	+
<i>Pneophyllum fragile</i> Kützing	R	+	-	-
<i>Polysiphonia furcellata</i> (C. Agardh) Harvey	R	+	+	+
<i>Polysiphonia scopulorum</i> Harvey	R	+	+	+
<i>Polysiphonia</i> sp. 1	R	+	+	+
<i>Polysiphonia</i> sp. 2	R	+	+	+
<i>Pringsheimiella scutata</i> (Reinke) Höhnelt ex Marchewianka	C	+	+	+
<i>Pterosiphonia ardeana</i> Maggs & Hommersand	R	+	+	+
<i>Pterosiphonia pinnulata</i> (Kützing) Maggs & Hommersand	R	+	+	+
<i>Pterothamnion crispum</i> (Ducluzeau) Nägeli	R	+	+	+
<i>Pterothamnion plumula</i> (J. Ellis) Nägeli	R	+	+	+
<i>Radicilingua thysanorhizans</i> (Holmes) Papenfuss	R	+	+	+
<i>Rhodophyllis divaricata</i> (Stackhouse) Papenfuss	R	+	+	+
<i>Rhodymenia ardissoni</i> Feldmann	R	+	+	+
<i>Sahlingia subintegra</i> (Rosenvinge) Kornmann	R	+	+	+
<i>Seirospora apiculata</i> (Meneghini) G. Feldmann-Mazoyer	R	-	+	-
<i>Seirospora sphaerospora</i> Feldmann	R	+	+	+
<i>Spermothamnion flabellatum</i> Bornet	R	+	-	-
<i>Spermothamnion irregulare</i> (J. Agardh) Ardissoni	R	+	+	+
<i>Spermothamnion repens</i> (Dillwyn) Rosenvinge	R	+	+	-
<i>Sphacelaria cirrosa</i> (Roth) C. Agardh	O	+	+	+
<i>Sphacelaria plumula</i> Zanardini	O	+	+	+
<i>Sphondylothamnion multifidum</i> (Hudson) Nägeli	R	+	+	+
<i>Sporochnus pedunculatus</i> (Hudson) C. Agardh	O	+	+	-
<i>Spyridia filamentosa</i> (Wulfen) Harvey	R	+	+	+
<i>Stylonema alsidii</i> (Zanardini) K. Drew	R	+	+	+
<i>Stylonema cornu-cervi</i> Reinsch	R	+	+	+
<i>Stypocaulon scoparium</i> (Linnaeus) Kützing	O	+	+	+
<i>Taonia atomaria</i> (Woodward) J. Agardh	O	-	+	-
<i>Titanoderma pustulatum</i> (J.V. Lamouroux) Nägeli	R	+	+	+
<i>Ulva clathrata</i> (Roth) C. Agardh	C	+	-	-
<i>Ulva rigida</i> C. Agardh	C	+	-	-
<i>Uronema</i> sp.	C	+	+	+
<i>Urospora laeta</i> (Thuret ex Bornet) Børgesen	C	+	+	+
<i>Valonia utricularis</i> (Roth) C. Agardh	C	+	+	-
<i>Womersleyella setacea</i> (Hollenberg) R.E. Norris	R	+	+	+
<i>Wrangelia penicillata</i> (C. Agardh) C. Agardh	R	+	+	+