

# The role of disturbance in promoting the spread of the invasive seaweed *Caulerpa racemosa* in seagrass meadows

Giulia Ceccherelli · Stefania Pinna ·  
Valentina Cusceddu · Fabio Bulleri

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**Abstract** Human disturbances, such as anchoring and dredging, can cause physical removal of seagrass rhizomes and shoots, leading to the fragmentation of meadows. The introduced green alga, *Caulerpa racemosa*, is widely spread in the North-West Mediterranean and, although it can establish in both degraded and pristine environments, its ability to become a dominant component of macroalgal assemblages seems greater in the former. The aim of this study was to estimate whether the spread of *C. racemosa* depends on the intensity of disturbance to the canopy structure of *Posidonia oceanica*. A field experiment was started in July 2010 when habitat complexity of a *P. oceanica* meadow was manipulated to simulate mechanical disturbances of different intensity: rhizome damage (High disturbance intensity = H), leaf removal (Low disturbance intensity = L), and undisturbed (Control = C). Disturbance was applied within plots of different size (40 × 40 cm and 80 × 80 cm), both inside and at the edge of the *P. oceanica* meadow, according to an orthogonal multifactorial design. In November 2011 (16 months after the start of the

experiment), no *C. racemosa* was found inside the seagrass meadow, while, at the edge, the cover of the seaweed was dependent on disturbance intensity, being greater where the rhizomes had been damaged (H) than in leaf removal (L) or undisturbed (C) plots. The results of this study indicate that physical disturbance at the margin of seagrass meadows can promote the spread of *C. racemosa*.

**Keywords** Canopy · *Caulerpa racemosa* · Edge effects · Introduced species · Invasion · *Posidonia oceanica* · Resistance

## Introduction

Several factors have been identified as pivotal in determining the establishment and spread of non-native invasive species (see reviews by Airoldi 1998; Richardson et al. 2000; Dietz and Edwards 2006; Theoharides and Dukes 2007). Because the diversity of extant native communities and structured habitats has been considered as an important barrier for invasion (Byers 2002; Predick and Turner 2008), anthropogenic disturbance is considered as an invasion promoter (Richardson et al. 2000; Bulleri et al. 2010). Removal of biomass due to disturbance can favour the establishment of nonindigenous species by reducing competition from natives and/or by enhancing resource availability (Davis et al. 2000; Mack et al. 2000; Johnston and Keough 2002; Shea and Chesson

G. Ceccherelli (✉) · S. Pinna · V. Cusceddu  
Dipartimento di Scienze della Natura e del Territorio,  
Polo Bionaturalistico, University of Sassari, Via  
Piandanna 4, 07100 Sassari, Italy  
e-mail: cecche@uniss.it

F. Bulleri  
Dipartimento di Biologia, University of Pisa, Via Derna 1,  
56126 Pisa, Italy

2002). Although this disturbance-invasion paradigm is not always supported by empirical studies (e.g. Lohrer et al. 2008), correlative and manipulative studies have extensively shown a positive relationship between ecosystem invasibility and disturbance, both in terrestrial and marine ecosystems (Hobbs and Huenneke 1992; D'Antonio and Vitousek 1992; Clark and Johnston 2011; Tamburello et al. 2014).

In marine environments, habitat-forming macrophytes regulate ecosystem processes by dominating primary production (Paine 2002), increasing habitat complexity and modifying the environment for associated organisms (Dayton 1975; Bruno et al. 2003). The endemic seagrass *Posidonia oceanica* (L.) Delile is a key species in Mediterranean coastal ecosystems (Pergent 1992), experiencing a widespread decline throughout the basin (Pérès 1984; Boudouresque et al. 1990; Peirano and Bianchi 1997; Boudouresque 2003). The regression of seagrass beds and the consequent expansion of alternative habitats (e.g. algal turfs or dead seagrass rhizomes generally referred to as “dead matte”) have been documented adjacent to urban areas worldwide (Boudouresque et al. 2009; Waycott et al. 2009; Montefalcone et al. 2010; Tamburello et al. 2012). Among the various human activities responsible for seagrass regression, direct mechanical damage from various fishing activities (e.g. trawling, gillnetting), anchoring (Ardizzone et al. 2006; Ceccherelli et al. 2007; Montefalcone et al. 2008) and dredging can cause physical removal of seagrass rhizomes and shoots, reducing habitat complexity and, thus, species diversity. Introduced species have also often been implicated in seagrass declines, but the evidence for negative effects on seagrasses is largely correlative (Glasby 2013 for a review), and in general, invasions by macroalgae occur in seagrass meadows already exposed to human perturbations (Bulleri et al. 2011). Given the limited experimental evidence, it thus remains unclear if macroalgal invasions are “drivers” of seagrass declines or instead “passengers” (Bulleri et al. 2010) that are responding opportunistically to degradation of seagrass beds caused by other disturbances (Williams 2007; Glasby 2013).

Species of the genus *Caulerpa* are the best known macroalgal invaders of seagrass beds (Williams and Smith 2007). *Caulerpa racemosa* is widely spread in the northwestern Mediterranean, where it has established in different habitats, at depths ranging from 0 to

40 m (Ceccherelli et al. 2002; Piazzini et al. 2005; Ruitton et al. 2005; Piazzini and Balata 2009). Correlative evidence suggests that *P. oceanica* meadows fragmented or characterized by low shoot densities are more heavily colonised by *C. racemosa* (Katsanevakis et al. 2010; Bulleri et al. 2011). In particular, Katsanevakis et al. (2010) found a low occurrence of *C. racemosa* inside intact meadows, with the macroalga mostly restricted to the margins of seagrass meadows or to gaps within disturbed meadows. In addition, experimental evidence indicates that the growth of *C. racemosa* at the edge of seagrass meadows is regulated by *P. oceanica*: stolon elongation and percent cover of *C. racemosa* were significantly higher where *P. oceanica* shoot density was reduced to 10 % of the natural density (Ceccherelli et al. 2000).

Thus, disturbance to seagrass shoots due to anchoring or fishing activities (trawling, gillnetting) could promote the establishment and/or spread of *C. racemosa* into seagrass beds (Francour et al. 1999; Milazzo et al. 2004; Ceccherelli et al. 2007; Montefalcone et al. 2007). Gaps in *P. oceanica* beds are likely to create favorable microhabitats for the settlement and spread of *C. racemosa* (Kiparissis et al. 2011). *C. racemosa* is, in fact, able to colonize space through both vegetative growth of prostrate stolons and settlement of current-borne fragments (Piazzini and Cinelli 1999). However, while several descriptive studies have documented the presence of *C. racemosa* in degraded *P. oceanica* habitats (Katsanevakis et al. 2010; Bulleri et al. 2011), except for the study of Ceccherelli et al. (2000), there has been no experimental investigation of how mechanical disturbance can promote the spread of this macroalga into *P. oceanica* meadows.

The aim of this study was to estimate whether the spread of *C. racemosa* depends on the intensity of disturbance on the canopy structure of the seagrass and the location of the disturbance within the seagrass bed. We mimicked the damage provoked by mechanical human disturbance on the seagrass canopy structure by inflicting different disturbance intensities (rhizome damage, leaf removal and undisturbed) to areas of different size and thus simulating damage due to human activities, such as anchoring or gillnet operation, of variable extent. *C. racemosa* can colonize space at the edge of meadows through both vegetative propagation from invaded area at the margins and supply of fragments from the water column.

Differently, only the latter mechanism can promote space colonization by *C. racemosa* inside meadows. Thus, the different combinations of intensity and extent of disturbance were applied inside and at the edge of the meadow. Specifically, we tested the hypotheses that the spread of *C. racemosa* would be greater (1) under high intensity of disturbance, (2) in larger disturbed patches and (3) at the edge rather than inside the meadow.

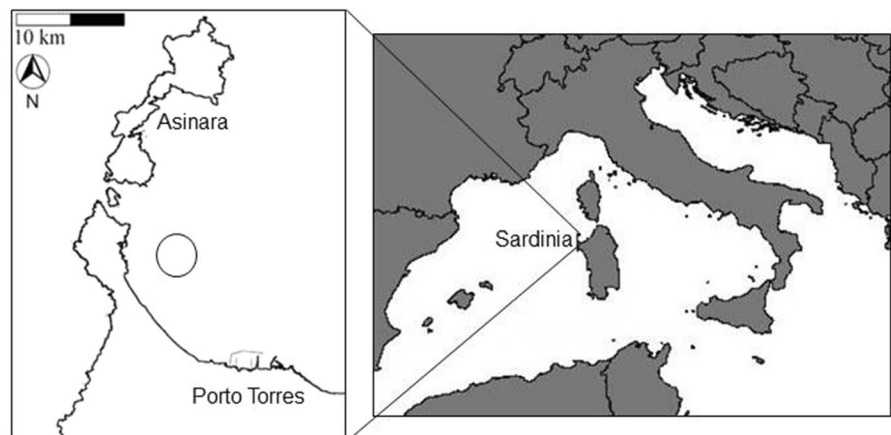
## Materials and methods

The study was done in the Asinara Gulf (northwestern tip of Sardinia, 40° 51.878N and 8° 20.290E), in the area between the town of Porto Torres and the Asinara Island MPA (Fig. 1). At our study site, continuous *P. oceanica* meadows occurred from shallow waters to about 40 m of depth. Canopy structure of the seagrass in this area seemed relatively well preserved, with shoot densities of  $176.4 \pm 14.2$  and  $237.0 \pm 20.0$  shoots  $\text{m}^{-2}$  (mean  $\pm$  SE;  $n = 48$ ) in the inner meadow and at the edge, respectively (the difference in structure is due the presence of orthotropic and plagiotropic rhizomes at the edge of the meadow; Hemminga and Duarte 2000). Leaf lengths (see Results) corresponded generally with those reported from areas not exposed to major human disturbance (Pergent et al. 1995). Rhizomes of the plants are mostly orthotropic, and areas of dead matte were not common. At this site, *C. racemosa* has been spreading for about 15 years, and at the time of the study, it had become common on rocky reefs, on dead matte of *P. oceanica* and at the margin of meadows (Bulleri et al. 2011). The presence of the

macroalga in discontinuities of the meadow, probably caused by mechanical damage from illegal trawling, was quite common (authors' personal observation).

A field experiment was started in July 2010, when habitat complexity of a *P. oceanica* bed, about 5 m deep, was manipulated to simulate the effects of mechanical disturbances of different intensity: rhizome damage (High disturbance intensity = H), leaf removal (Low disturbance intensity = L), and undisturbed (Control = C). The high disturbance intensity consisted in the damaging of rhizomes through the cutting of all the shoots under the basal meristem (not allowing leaf re-growth), while the low level was obtained by cutting shoots over the basal meristem (allowing leaf re-growth). Disturbance was applied at two positions of the seagrass meadow: inside and at the edge of the meadow. For the latter position, one side of each plot was open to the adjacent rocky platform, which had already been invaded by *C. racemosa* (site-wide cover in July 2010 was  $58.7 \pm 9.1$  % (mean  $\pm$  SE), based on 25 haphazardly-placed 400  $\text{cm}^2$  quadrats). Colonization of plots at the edge could, thus, occur directly by clonal spread from the adjacent area. We did not, however, measure the abundance or distribution of *C. racemosa* in the area adjacent to each individual plot, and unfortunately, due to the sampling frequency of our experiment, we could not determine if the colonization of any individual plot was due to clonal growth or the settlement of fragments. Disturbance treatments were applied to plots (i.e., the experimental units) of different size (small 40  $\times$  40 cm and large 80  $\times$  80 cm), according to an orthogonal multifactorial design. Plots were interspersed within the same *P. oceanica* bed: edge

**Fig. 1** Study site in the Asinara Gulf (NW Sardinia)



plots followed the contour of the bed, while plots inside the bed were established about 5 m from the edge. Three replicate plots were established for each combination of position, plot size and intensity of disturbance. There was no *C. racemosa* in any of the plots at the beginning of the study.

Leaf length in the low disturbance plots was quantified at three different times (July 2010, about 3 weeks after the start of the experiment, November 2010 and May 2011), by measuring the longest leaf of five shoots chosen at random within each experimental unit (=plot). Data taken on the last time were analysed by four-way ANOVA including the factors 'position' (edge and inside), 'size' of the plots (small and large), 'intensity' of disturbance (H, L, and C), and 'experimental unit' (nested in the interaction 'position  $\times$  size  $\times$  disturbance'). No regrowth of the leaves was observed where the meristem of the rhizome was damaged (H).

In order to obtain a comprehensive assessment of the response of *C. racemosa* to experimental conditions, its cover was quantified both on the bottom of plots and on *P. oceanica* rhizomes. The cover of *C. racemosa* on the bottom of each plot was quantified at four different times (August, October 2010, May and November 2011), by photographing the sedimentary substrate (25  $\times$  25 cm surface). The cover of the *C. racemosa* on rhizomes was estimated at three different times (November 2010, May and December 2011) by photographing five randomly-selected rhizomes for each experimental plot. Photographs were taken using a digital camera (Canon S70) equipped with a waterproof case (Canon WPDC40) and a metal spacer and framer. The percentage cover of *C. racemosa* on the substrate was estimated visually on a computer screen: a grid of twenty-five sub-quadrats was superimposed onto each image and a score from 0 to 4 % was given in each sub-quadrat, and the percentage cover estimated by summing over the entire set of sub-quadrats (Dethier et al. 1993). Similarly, the percentage cover of *C. racemosa* on the rhizomes was estimated by using a vertical rectangular grid of twenty sub-quadrats (2  $\times$  10) giving a score from 0 to 5 % to each sub-quadrat, adapting the grid to the rhizome size. Rhizomes shorter than 3 cm were not included in the sampling.

*C. racemosa* did not colonize plots inside the meadows. Analyses on the abundance of the seaweed were, therefore, restricted to data from the edge. The

cover of *C. racemosa* on the substrate and on rhizomes was analysed by means of a two-way ANOVA including the factors 'size of the plot' (small and large) and 'intensity' of disturbance (H, L, and C), treated as fixed and orthogonal. Cochran's test was performed to check for homogeneity of variances, while SNK test was utilized to make a posteriori comparisons of mean values (Underwood 1997).

## Results

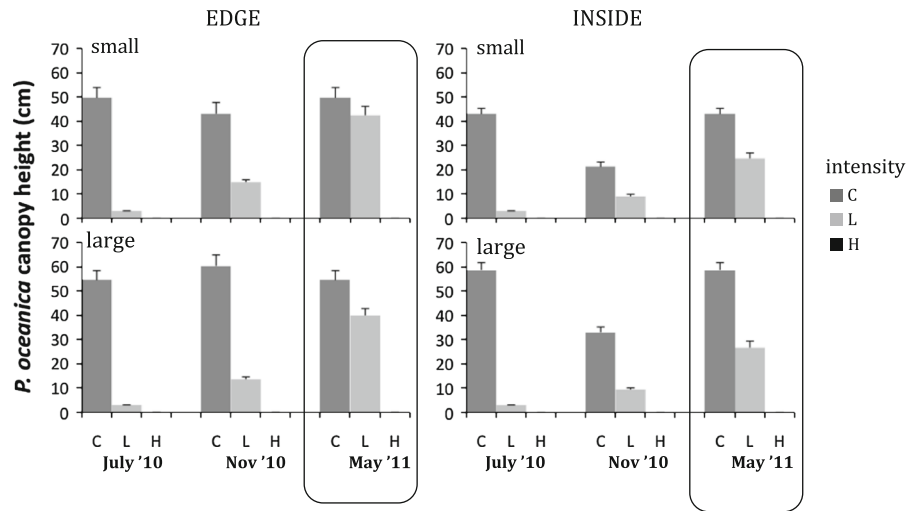
The structure of *P. oceanica* canopy was affected by disturbance treatments, although there was large variability among plots. In plots exposed to high intensity of disturbance, no re-growth was observed during the study period after the initial removal of all leaves in July 2010 (Fig. 2). Although the recovery of the plants exposed to a low intensity of disturbance was appreciable, the height of the canopy was lower than in control plots, independent of the size of the plot (significant Size  $\times$  Intensity and SNK test in Table 1; Fig. 2).

*C. racemosa* was never found in plots inside the meadow, either on the substrate or on *P. oceanica* rhizomes. In contrast, at the edge of the meadow, *C. racemosa* colonized all the plots, although its abundance on the substrate and rhizomes depended on the intensity of disturbance (Table 2; Fig. 3): at the end of the study, the cover of *C. racemosa* on the substrate in plots exposed to high disturbance intensity was greater than in those exposed to low disturbance or undisturbed controls (SNK tests in Table 2): graphical inspection suggests that, through time, the re-growth of the canopy reduced the abundance of *C. racemosa* in low disturbance intensity plots. The size of the plot did not affect the cover of *C. racemosa* on the substrate, but it did influence the occurrence on *P. oceanica* rhizomes, although cover values were generally low (Table 2). *C. racemosa* cover on rhizomes was, in fact, appreciable only in large, highly disturbed plots at the edge of the meadow (significant Size  $\times$  Intensity and SNK test in Table 2).

## Discussion

In NW Sardinia, patterns of occurrence of *C. racemosa* among areas subjected to different human

**Fig. 2** Mean (+SE) *P. oceanica* canopy height (cm) at the edge and inside the meadow at the three sampling times (July–November 2010 and May 2011) for the three disturbance levels: High intensity (H), Low (L) and Controls (C) in the small (40 × 40 cm) and large (80 × 80 cm) plots. The last sampling time has been used for the analysis



**Table 1** Results of 4-way ANOVA on the canopy height on the last sampling time

Source of variation	df	MS	F	P
Position = P	1	498.33	2.09	0.1617
Size = S	1	1,397.23	5.85	<b>0.0236</b>
Intensity = I	2	40,789.5	170.67	<b>0.0000</b>
Exp unit (P × S × I)	24	239.00	2.92	<b>0.0000</b>
P × S	1	297.73	1.25	0.2754
P × I	2	536.71	2.25	0.1276
S × I	2	1,110.79	4.65	<b>0.0197</b>
P × S × I	2	111.64	0.47	0.6324
Residual	144	81.77		
Cochran's		C = 0.120	P > 0.05	
SNK test		Size Intensity		
SE = 2.82		small = large C		
S × I		small < large L		
		0 = 0 H		
		small C > L > H		
		large C > L > H		

The effect of Position within the seagrass (inside = In and edge = Ed), Size of disturbance (small = 40 × 40 cm and large = 80 × 80 cm), Disturbance (High intensity = H, Low intensity = L, and C = control) and experimental unit (nested in the interaction P × S × I) are indicated. Significant values are in bold. SNK test indicated alternative hypotheses for the interaction S × I

influences have been found to match variations in the relative proportion of favourable and unfavourable habitats (Bulleri et al. 2011). Degraded habitats, such as dead *P. oceanica* rhizomes or macroalgal turfs, are more vulnerable to be colonized by *C. racemosa*,

while structured habitats, such as seagrass beds and stands of canopy-forming macroalgae, can act as a barrier against the spread of this introduced seaweed (Bulleri et al. 2010). The experimental results of this study suggest that physical disturbance clearing the canopy promotes the spread of *C. racemosa* at the margin of seagrass meadows. Our prediction that invasion success of *C. racemosa* would have been greater under a higher intensity of disturbance was confirmed.

In particular, the marked re-growth of leaves in low-disturbance plots, both small and large in size, can thus reduce the spread and reattachment of fragments of *C. racemosa*. *C. racemosa* was able to spread rapidly into low-disturbance plots shortly after the beginning of the experiment, when the canopy had not re-grown yet, indicating a 3-month response of the macroalga to the availability of free space. However, over time, the cover of the macroalga in low-disturbance plots declined and was not different from controls by the end of the experiment. In contrast, in high-disturbance plots *C. racemosa* cover was initially much lower but increased steadily during the course of the experiment. Thus, the availability of free space is apparently not the only factor driving initial colonization rates since high and low disturbance intensity should have then supported similar covers of *C. racemosa* shortly after disturbance treatments were applied (August 2010). Nevertheless, a clear effect of the disturbance intensity emerged by the end of the experiment (November 2011), although the temporal trend among treatments seemed different especially

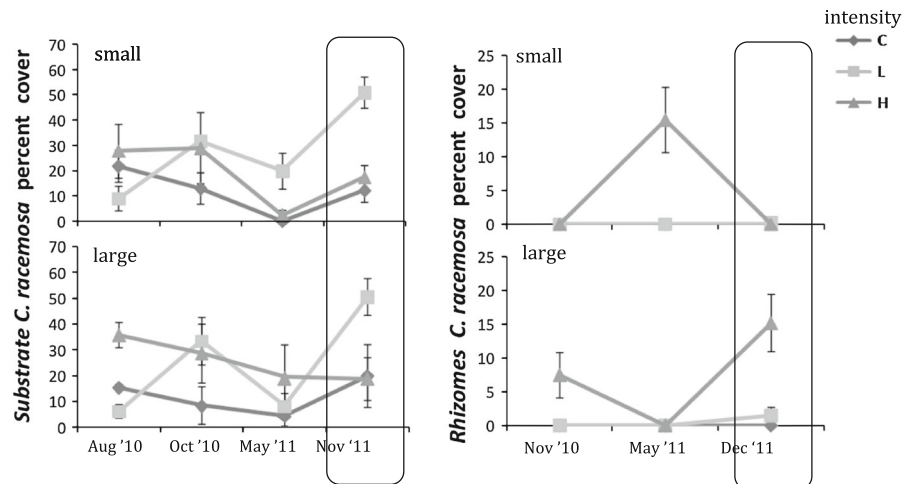


**Table 2** Results of 2-way ANOVA on *C. racemosa* percent cover at the last sampling time

Source of variation	<i>Caulerpa</i> cover substrates				<i>Caulerpa</i> cover rhizomes			
	df	MS	F	P	df	MS	F	P
Size = S	1	37.55	0.22	0.6479	1	675.13	13.91	<b>0.0003</b>
Intensity = I	2	2,279.23	13.31	<b>0.0009</b>	2	258.42	10.65	<b>0.0000</b>
S × I	2	26.58	0.16	0.8579	2	265.53	10.94	<b>0.0000</b>
Residual	12	171.21			84	48.53		
Cochran's transf		C = 0.421	ns			C = 0.924	none	P < 0.01
<b>SNK test</b>	C = L < H				<b>SNK test</b>	small = large C		
Intensity					S × I	small = large L		
SE = 5.34					SE = 1.79	small < large H		
						small C = L = H		
						large C = L < H		

The effect of size of disturbance (small = 40 × 40 cm and large = 80 × 80 cm) and disturbance (High intensity = H, Low intensity = L, and control = C) are indicated. Significant values are in bold. SNK test indicates alternative hypotheses

**Fig. 3** Mean (±SE) *C. racemosa* percent cover through the study period on the substrate (left) and on the rhizomes (right) at the edge of the meadow for the High intensity (H), Low intensity (L), and Controls (C) in the small (40 × 40 cm) and large (80 × 80 cm) plots. The last sampling time has been used for the analysis. *C. racemosa* cover inside the meadow was zero and not plotted



until October 2010. In all treatments, the cover of *C. racemosa* decreased in winter and spring 2011 and then increased through the summer until November 2011, reflecting seasonal effects on its growth dynamics in this region of the Mediterranean (e.g. Ceccherelli et al. 2000; Piazzini et al. 2001).

Several mechanisms can be responsible for *C. racemosa* failing to spread into undisturbed and low disturbance intensity of *P. oceanica* canopy. The presence of the canopy can directly or indirectly affect the environment underneath it and influence the invasion success. For example, sweeping of the substrate by leaves, may prevent the establishment of understory species, as documented by Irving and

Connell (2006) in kelp forests. Alternatively, reduced *C. racemosa* spread might be the result of a reduction in irradiance under the canopy. Whatever the mechanism, the results of this study provide support to previous correlative and manipulative evidence of a better ability of *C. racemosa* to colonize poorly structured seagrass architecture: vertical and horizontal *C. racemosa* growth is negatively influenced by dense and healthy *P. oceanica* meadows (Ceccherelli et al. 2000; Klein and Verlaque 2008; Katsanevakis et al. 2010). In contrast, in fragmented seagrass meadows, sand or mat patches are vulnerable to *C. racemosa* invasion (Katsanevakis et al. 2010; Bulleri et al. 2011; Kiparissis et al. 2011). In addition, this seaweed has often been

found growing along the rhizomes inside sparse meadows (Klein and Verlaque 2008).

The physical and biological characteristics of a local patch of habitat and of the surrounding landscape can both be important determinants of habitat occupancy (Pearson 1993; Wiens et al. 1993; Ricketts 2001; Thomas et al. 2001; Driscoll 2007). Thus, the structure of *P. oceanica* canopy in the experimental plots may not be the only factor regulating establishment and spread of *C. racemosa*. The neighbour habitat and the seascape may change the probability for a seagrass patch of poor structure to be colonised by preventing species spread. However, the results of this study suggest that gaps of disturbed *P. oceanica* inside the meadow would not enhance the establishment of *C. racemosa*. Indeed, inside the meadow, *C. racemosa* was found neither in large nor in small size gaps created with high disturbance intensity suggesting that this type of localized and sparse clearances do not promote the establishment of the macroalga. Although 'uprooted' fragments of *C. racemosa* can easily re-attach to the substrate (Ceccherelli and Piazzini 2001; Piazzini et al. 2003), we believe that in such gaps the buffer effect of the surrounding canopy can contrast or delay the arrival of fragments that, being not-buoyant (Ceccherelli and Piazzini 2001), have reduced chances to reach such gaps. Thus, only a small proportion of drifting fragments transported by waves or currents reach these gaps, as they are likely to be retained by seagrass rhizomes at the margin of the meadow. However, at the edge of the meadow, we were not able to tease apart the relative contribution of the supply of fragments from the water column from that of clonal growth in determining colonization success of *C. racemosa*. However, the clonal growth habit of *C. racemosa* and its high abundance in areas adjacent to the meadow edge (>50 % cover) makes it likely that the greater colonization of disturbed edge plots was due to clonal growth of established individuals. Further experiments are required to isolate the relative contribution of the two mechanisms that potentially account for colonization of space at the edge of seagrass meadows. These experiments would imply the removal of *C. racemosa* in the area surrounding disturbed *P. oceanica* plots, so that recorded colonization could be reliably ascribed to the settlement of algal fragments from the water column.

Further, for the spread of the macroalga on rhizomes, the size of disturbance seems as important as the

intensity of disturbance, highlighting that the larger the size the greater would be the invasion. This supports the hypothesis that the degree of the invasion of the seagrass might also change depending on the extension of disturbance and would be more rapid when disturbance is distributed over large areas. Although analyses of long-term invasion dynamics in disturbed seagrass habitats are lacking, our results suggest that *C. racemosa* is a passenger of changes in *P. oceanica* habitat rather than a driver, supporting previous experimental evidence from rocky reefs (Bulleri et al. 2010). However, this is not necessarily in opposition to evidences that the level of interaction between *P. oceanica* and *C. racemosa* significantly modifies the vegetative development of the seagrass (Dumay et al. 2002) and that the withdrawal of *P. oceanica* from the disturbed areas that have been colonized by *C. racemosa* may be permanent, due to high colonization potential of the macroalga and its phytotoxic properties (Kiparissis et al. 2011 and reference therein).

In conclusion, although the effect of seascape structure on invasion biology of the macroalga is still to be defined, disturbed *P. oceanica* patches enhance the occupancy and the spread of *C. racemosa*. Mechanical human disturbance of *P. oceanica* is weakly managed, as poaching occurs and measures of surveillance are inadequate. As a consequence, damage due to trawling is relatively common, while use of gillnets or anchoring is managed locally only for the specific objectives of marine protected areas. According to our results, management measures for protecting seagrass meadows and the biodiversity they host from mechanical disturbance would indirectly hinder the spread of *C. racemosa*. Determining which management scenario will best control invasive species will depend on their relative efficacy in protecting vulnerable habitats and raising of public awareness.

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