

# Propagules are not all equal: traits of vegetative fragments and disturbance regulate invasion success

MARC UYA,<sup>1,2</sup> FABIO BULLERI,<sup>1,3</sup> AND PAUL E. GRIBBEN<sup>2,4,5</sup>

<sup>1</sup>*Dipartimento di Biologia, Università di Pisa, Via Derna 1, Pisa 56126 Italy*

<sup>2</sup>*Centre for Marine Bio-Innovation, School of Biological, Earth and Environmental Sciences, University of New South Wales, New South Wales 2052 Australia*

<sup>3</sup>*CoNISMa, Consorzio Nazionale Interuniversitario per le Scienze del Mare, Piazzale Flaminio 9, Roma 00196 Italy*

<sup>4</sup>*Sydney Institute of Marine Science, 19 Chowder Bay Road, Mosman, New South Wales 2088 Australia*

**Abstract.** Invasion success is regulated by multiple factors. While the roles of disturbance and propagule pressure in regulating the establishment of non-native species are widely acknowledged, that of propagule morphology (a proxy for quality) is poorly known. By means of a multi-factorial field experiment, we tested how the number (5 vs. 10) and quality (intact, without fronds or without rhizoids) of fragments of the clonal invasive seaweed, *Caulerpa cylindracea*, influenced its ability to establish in patches of the native seagrass, *Posidonia oceanica*, exposed to different intensities of disturbance (0, 50, or 100% reduction in canopy cover). We hypothesized that the ability of fragments to establish would be greater for intact fragments (high quality) and reduced more by frond removal (low quality) than rhizoid removal (intermediate quality). At low propagule pressure or quality, fragment establishment was predicted to increase with increasing disturbance, whereas, at high propagule pressure or quality, it was predicted to be high regardless of disturbance intensity. Disturbance intensity, fragment number and quality had independent effects on *C. cylindracea* establishment success. Disturbance always facilitated fragment establishment. However, fragments retaining fronds, either intact or deprived of rhizoids, had higher establishment success than fragments deprived of fronds. Increasing propagule number had weak effects on the cover of *C. cylindracea*. Our results demonstrate that propagule traits enabling the acquisition of resources made available by disturbance can be more important than propagule number in determining the establishment and spread of clonal non-native plants. More generally, our study suggests that propagule quality is a key, yet underexplored, determinant of invasion success.

**Key words:** *biological invasion; biotic resistance; Caulerpa cylindracea; clonal seaweeds; disturbance; propagule pressure; propagule quality.*

## INTRODUCTION

Understanding the mechanisms that underlie biological invasions, one of the major causes of biodiversity loss worldwide (Mack et al. 2000, Dextrase and Mandrak 2006), is key to predicting habitats vulnerable to future invasions. Many factors, such as features of the recipient native community, disturbance regimes, the biology and ecology of the invasive species and its associated propagule pressure, can regulate the success of invasive species (D'Antonio and Vitousek 1992, Davis et al. 2000, Stachowicz et al. 2002, Lockwood et al. 2005). However, manipulative experimental studies have generally focused on only one of these factors, despite compelling evidence indicating that invasion success is likely dependent on interactions among them (Leung and Mandrak 2007, Britton-Simmons and Abbott 2008, Clark and Johnston 2009, Eschtruth and Battles 2009).

Disturbance to native communities is often a key determinant of invasion success (Davis et al. 2000). For example, disturbance to native canopies can release non-native plants from biotic resistance by providing access to limited resources such as light and space (Elton 1958, Hobbs and

Huenneke 1992, Stachowicz et al. 2002, Corbin and D'Antonio 2004, Bulleri et al. 2010, Byun et al. 2017). However, the effects of increased resource availability (Davis et al. 2000) can interact with invader propagule pressure to determine invasion success (D'Antonio et al. 2001, Thomsen et al. 2006, Britton-Simmons and Abbott 2008, Byun et al. 2015). For instance, disturbance to native fouling communities fostered the establishment of the invasive bryozoan *Watersipora suborquata* only when it occurred in association with high propagule pressure (Clark and Johnston 2009). Likewise, in a Californian coastal grassland, decreased biotic resistance due to higher springtime water availability amplified the positive effects of increased propagule pressure on the establishment of the European perennial grass *Holcus lanatus* (Thomsen et al. 2006). On the other hand, resistance to invasion can be overwhelmed by high invader propagule pressure, irrespective of disturbance levels (Hollebone and Hay 2007, 2008). For example, high propagule pressure of the Japanese stiltgrass, *Microstegium vimineum*, overwhelmed the resistance to invasion of a deciduous forest ecosystem (Warren et al. 2012). Thus, disturbance might be essential for invader establishment when propagule pressure is low, but have weaker effects when propagule pressure is high.

An overlooked factor influencing the success of invasive species is propagule quality (here referred to as the physical condition, such as the morphology or biomass of a propagule). For example, the settlement, metamorphosis and

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<sup>5</sup>E-mail: [p.gribben@unsw.edu.au](mailto:p.gribben@unsw.edu.au)

performance of the larvae of some invasive marine invertebrates increase with their body size (Marshall and Keough 2003, Marshall et al. 2003, 2006). Likewise, the number and size of internodes on rhizome fragments of invasive clonal plants with vegetative reproduction significantly affect their settlement and expansion dynamics (Quinn and Holt 2008, Estrada et al. 2016). Production of these propagules by biotic or abiotic disturbance results in fragments of differing size/biomass or containing different morphological components (e.g., combinations of roots/shoots/leaves) that are essential for acquiring different resources (leaves or fronds for photosynthesis; roots for nutrient uptake). Thus, the presence/absence of different morphological components - which may generate fragments of different quality - could be as important as propagule number in regulating individual fragment success (Estrada et al. 2016). Disturbance is, in fact, unlikely to foster the establishment of plant fragments lacking those functional structures necessary for an efficient uptake of freed resources. Despite asexually reproducing plants being some of the most invasive species globally (Kaiser 2000, Allendorf and Lundquist 2003, Williams and Smith 2007), we know very little about how variations in the morphological characteristics of vegetative fragments interact with disturbance regimes to determine invasion success.

The clonal seaweed, *Caulerpa cylindracea* Sonder, (previously *Caulerpa racemosa* var. *cylindracea*), is among the most widespread non-native species in the Mediterranean Sea (Renoncourt and Meinesz 2002, Piazzini and Balata 2009). *C. cylindracea* colonizes a variety of habitats, including dead rhizomes of the native seagrass *Posidonia oceanica* (Linnaeus) Delile (Bulleri et al. 2011). Although intact seagrass meadows appear resistant to *C. cylindracea*, canopy removal can promote the establishment of *C. cylindracea* at their margins, suggesting a key role of disturbance in facilitating its establishment (Ceccherelli et al. 2014). *C. cylindracea* can reproduce sexually but mostly spreads through drifting asexual fragments generated by abiotic (i.e., wave surge and currents) or biotic disturbance (i.e., herbivore grazing; Ceccherelli et al. 2002, Klein and Verlaque 2008, Bulleri et al. 2009). Fragments vary not only in number but also in morphology since they can be formed by prostrate stolons carrying both fronds and rhizoids or lacking either one or both structures (authors' personal observation). In *Caulerpales*, rhizoids provide firm attachment to the substratum and allow nutrient uptake, while fronds are deputed to light harvesting (Komatsu et al. 1997, Chisholm and Moulin 2003). Therefore, the presence/absence of either rhizoids or fronds likely determines the response of *C. cylindracea* to disturbances increasing the availability of different resources. Importantly, however, enhanced uptake of nutrients may not foster establishment if photosynthetic efficiency is impaired by the absence or reduced density of fronds. Moreover, rhizoids, representing a smaller proportion of fragment biomass (Capiomont et al. 2005), can be re-generated more rapidly compared to fronds and their loss has less impact on fragment establishment than frond loss (Bulleri et al. 2018). Thus, fragments lacking rhizoids may generally be of higher quality than fragments lacking fronds.

Here, we experimentally evaluated how the quality and number of *C. cylindracea* fragments influenced its ability to establish in patches of *P. oceanica* exposed to disturbances of

varying intensity (i.e., amount of canopy removal). We predicted that: (1) the ability of fragments to establish would be greater for intact fragments (high quality) and that it would be reduced more by frond removal (low quality) than rhizoid removal (intermediate quality); (2) at either low propagule density or low fragment quality, fragment establishment would increase with increasing disturbance; (3) disturbance would have weaker effects on establishment success at either high propagule density or high fragment quality; (4) propagule quality would have stronger effects on fragment success compared to propagule number at any disturbance level.

## MATERIALS AND METHODS

### *Study system*

*Caulerpa cylindracea* is a clonal green alga considered one of the 100 most invasive species in the Mediterranean (Stefataris and Zenetos 2006). It was first recorded in Libya in 1990 and has now spread throughout the Mediterranean (see Klein and Verlaque 2008 for review). *C. cylindracea* occurs on a variety of habitats, from rocky shores to soft-sediments, and across a broad depth range, from the intertidal to 70 m of depth (Klein and Verlaque 2008, Bulleri et al. 2011).

*Posidonia oceanica* is one of the most important habitat-forming seagrass species in the Mediterranean, occurring across a broad depth range on sandy bottoms (Bethoux and Copinmontegut 1986). *P. oceanica* has leaves up to 70 cm long and forms large, dense beds that support high biodiversity and important fisheries (Ott 1980, Marbà et al. 1996, Guidetti 2000).

This study was conducted about 10 km south of Livorno (Antignano, 43°29'N, 10°19'E; NW Mediterranean), in a dense subtidal *P. oceanica* seagrass meadow (1 ha × 1.5 ha, mean ± SE shoots per m<sup>2</sup> = 316.4 ± 11.5; M. Uyà unpublished data), occurring at 4–8 m water depth and surrounded by a matrix of boulder and sandy substrata. *C. cylindracea* is abundant at this site, often occurring along the margins of the seagrass meadow.

### *Effects of disturbance, propagule quality and pressure on C. cylindracea establishment*

We experimentally tested the effects of disturbance intensity (3 levels; canopy intact, 50% canopy reduction and 100% canopy reduction), propagule pressure (2 levels; 5 and 10 fragments) and propagule quality (3 levels; intact fragments carrying both rhizoids and fronds, fragments lacking either rhizoids or fronds) on the establishment of *C. cylindracea*. Disturbance intensity treatments were created just before the peak in abundance of *C. cylindracea*, in mid-July (summer; Ruitton et al. 2005). We randomly established seventy-two 0.5 × 0.5 m plots at the margin of the *P. oceanica* meadow, at a depth of ~6 m. Plots had an initial seagrass cover of 100% and were scattered along a 170 m stretch of the meadow. Twenty four plots were then randomly assigned to either 0, 50, or 100% *P. oceanica* cover reduction (Fig. 1). In order to allow the seagrass to recover, reductions in canopy cover were achieved by cutting the leaves whilst leaving the rhizomes intact. Seagrass canopy cover in plots

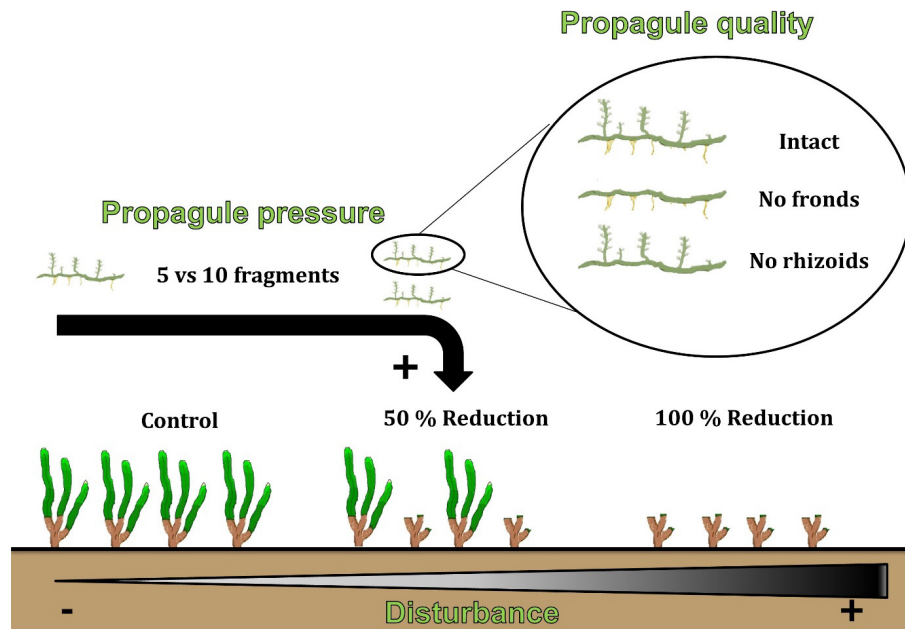


FIG. 1. Schematic diagram of the fully factorial experiment conducted in a *Posidonia oceanica* seagrass meadow investigating how disturbance intensity, propagule pressure and propagule quality regulate the establishment of *Caulerpa cylindracea* fragments. Four plots were assigned to each combination of disturbance intensity (3 levels), propagule pressure (2 levels) and propagule quality (3 levels), resulting in a total of 72 manipulated plots.

assigned to different disturbance intensity levels were maintained every 3 weeks throughout the duration of the experiment (10 weeks), by cutting re-grown leaves without disturbing *C. cylindracea* fragments.

Four plots for each level of disturbance were then randomly allocated to each of the six combinations of propagule pressure and quality (Fig. 1). Fragments of *C. cylindracea* (10 cm stolon length) were collected 2 d after the implementation of disturbance treatments from a nearby area (~100 m away from the experiment location) characterized by dead seagrass rhizomes. Either fronds or rhizoids were removed from fragments in the field, soon after their collection, using scissors. Either five or ten fragments were fixed with U-shaped metal staples within the central 20 × 20 cm area of each plot, to avoid edge effects ( $n = 540$  fragments in total). Plots were thoroughly searched for the presence of *C. cylindracea* before the experimental transplantation and, when present, it was removed. Both fronds and rhizoids represent a small proportion of the total biomass of the invasive seaweed (up to 12 × less biomass than the stolon; Capiomont et al. 2005), thus we controlled for initial propagule length, and not biomass, as differences between propagule morphologies in biomass were considered negligible. The attachment of all fragments was checked 2 d after they were transplanted to ensure all fragments had remained in place.

#### Sampling and data analysis

The percentage cover of *C. cylindracea* in each plot was visually estimated after three (August), six (September) and 10 weeks (October) from the start of the experiment, using a 20 × 20 cm plastic frame subdivided into 25 sub-quadrats. A score from 0 (absence) to 4 (completely covered) was given

to each sub-quadrat and the percentage cover was obtained by summing over the entire set of sub-quadrats (Dethier et al. 1993). At the end of the experiment, *C. cylindracea* fragments were retrieved from the central 20 × 20 cm area of each plot and brought to the lab for analysis. The total number of fronds, mean length of three randomly selected fronds, total stolon length and the number of rhizoids per quadrat were measured. Finally, total fragment biomass per quadrat was estimated as dry weight ( $g \cdot m^{-2}$ ) after drying the material at 60°C for 48 h.

The effects of canopy disturbance, propagule number and quality on the percentage cover of *C. cylindracea* were analyzed using a linear mixed-effects model. Seagrass disturbance intensity, propagule number and quality were considered as fixed effects. Time of sampling was considered as a random effect to take into account temporal auto-correlation in the data generated by repeatedly sampling the same quadrats. The baseline for the linear mixed model was set *a priori* as the, supposedly, most invasible scenario: the combination of 100% disturbance inoculated with 10 intact fragments. The analysis was performed in R (version 3.3.2) using the lme and anova functions within the nlme package (Pinheiro et al. 2018). When significant main effects were detected, multiple *post-hoc* Tukey's HSD tests were used to determine differences among the levels of disturbance intensity and propagule quality using the glht function within the multcomp package (Hothorn et al. 2013). Assumptions of linearity and variance homogeneity were checked by plotting the standardized residuals against fitted values (Zuur et al. 2009).

The effects of experimental conditions on the density and length of fronds, total stolon length, density of rhizoids and biomass of *C. cylindracea*, sampled at the end of the experiment, were analyzed by means of three-way ANOVA. The

model included canopy disturbance, propagule number and quality as fixed, crossed factors. Data were square root transformed when Cochran's test indicated significant heterogeneity of variances (Underwood 1997). Tukey's HSD tests were used for *post-hoc* comparison of the means. One plot assigned to the 100% seagrass cover reduction and transplanted with 10 intact fragments of *C. cylindracea* was lost at the start of the experiment. In order to maintain a balanced design, the missing value was replaced with the mean of the remaining replicates for this treatment and residual degrees of freedom were adjusted accordingly (Underwood 1997). All ANOVA tests were performed in R (version 3.3.2) using the *lm* function within the GAD package (Sandrini-Neto and Camargo 2012).

## RESULTS

Disturbance, propagule pressure and quality had significant effects on the cover of *C. cylindracea* in experimental plots (Fig. 2, Table 1). Across the study, the cover of the seaweed increased significantly with increasing disturbance intensity. In particular, the percent cover of the seaweed was, on average, 30 and 10 times higher in 100% and 50% canopy removals compared to control treatments, respectively, on the last sampling date (Fig. 2, Table 1).

The cover of *C. cylindracea* was significantly higher in plots inoculated with intact and no-rhizoid fragments than no-frond fragments (Fig. 2, Table 1) and increased with increasing

propagule pressure (Fig. 2, Table 1). When transplanted at high density (i.e., 10 fragments/plot), some intact and no-rhizoid fragments were also able to persist under intact canopies throughout the experiment. The interaction between disturbance and either propagule pressure or quality was non-significant, but only marginally so ( $P \leq 0.06$ , Table 1).

At the end of the experiment, the density of fronds and rhizoids, total stolon length and biomass increased with increasing intensity of disturbance (Figs. 3 and 4, Table 2 and Appendix S1: Fig. S1–S3). Moreover, total stolon length increased significantly with the number of fragments inoculated (Table 2, Appendix S1: Fig. S3). There was a significant effect of the interaction Disturbance  $\times$  Propagule quality on the mean length of fronds. The *post-hoc* tests indicated that fronds grew longer from intact and no-rhizoid fragments than no-frond fragments in 50% canopy reduction plots, while no differences occurred for the other disturbance levels (Table 2 and Appendix S1: Fig. S1).

The biomass of *C. cylindracea* was up to 50 $\times$  and 80 $\times$  higher in the 50% and 100% canopy cover reduction treatments, respectively, when compared to intact *P. oceanica*. In addition, in 100% canopy reduction plots inoculated with 5 fragments, final seaweed biomass was about 2.4 $\times$  higher for intact than no-fronds (Fig. 4, Table 2). Biomass was also significantly higher in plots inoculated with intact and no-rhizoid fragments than plots inoculated with no-frond fragments (Fig. 4, Table 2).

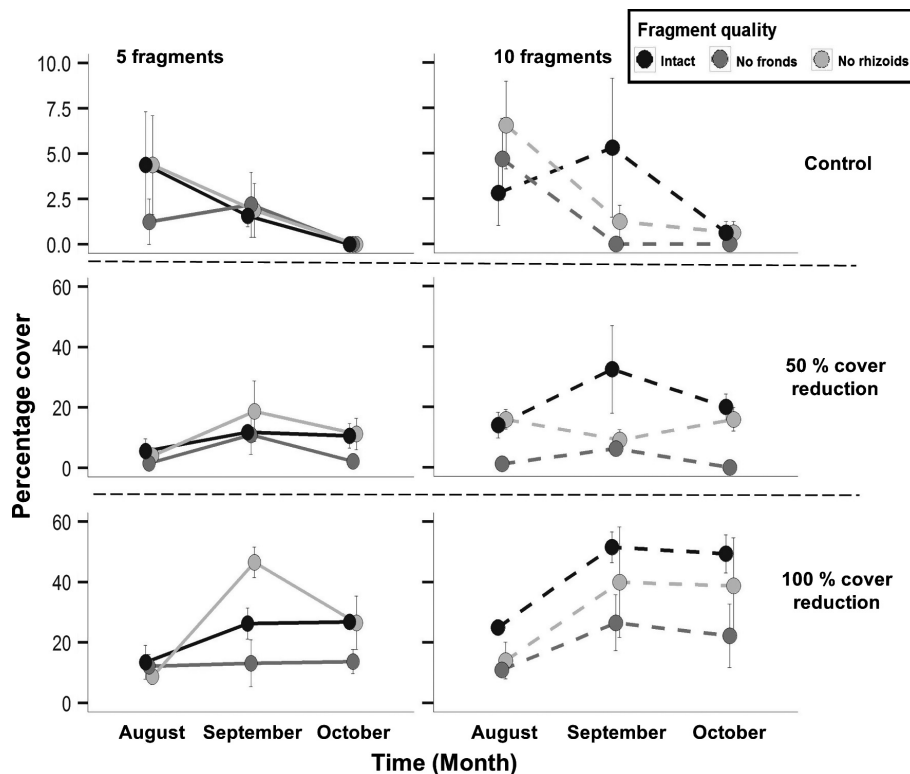


FIG. 2. Temporal trend of the percentage cover of *Caulerpa cylindracea* under different combinations of disturbance intensity, propagule pressure and propagule quality. Data are means  $\pm$  Standard Error. Continuous lines represent 5 fragment treatments whilst dashed lines indicate 10 fragment treatments. Differences in y-axes scale should be considered when comparing disturbance intensity levels.

TABLE 1. Linear mixed-effects model assessing the effects of disturbance intensity (*D*), propagule pressure (*P*) and propagule quality (*Q*) on the percentage cover of *Caulerpa cylindracea*. *Post-hoc* Tukey's HSD tests are reported when the main analysis showed significant effects of *D* or *Q*

	df	MS	F-value
Source of variation			
Disturbance intensity ( <i>D</i> )	2	10419.5	68.801***
Propagule pressure ( <i>P</i> )	1	1583.3	10.455**
Propagule quality ( <i>Q</i> )	2	1556.8	10.280***
<i>D</i> × <i>P</i>	2	436.1	2.880†
<i>D</i> × <i>Q</i>	4	327.3	2.161†
<i>P</i> × <i>Q</i>	2	268.2	1.77
<i>D</i> × <i>P</i> × <i>Q</i>	4	89.9	0.594
<i>post-hoc</i> Tukey HSD tests			
<i>D</i>		100% > 50% > Control	
<i>Q</i>		Intact = no rhizoids > no fronds	

†*P* ≤ 0.06; \**P* < 0.05; \*\**P* < 0.01; \*\*\**P* < 0.001.

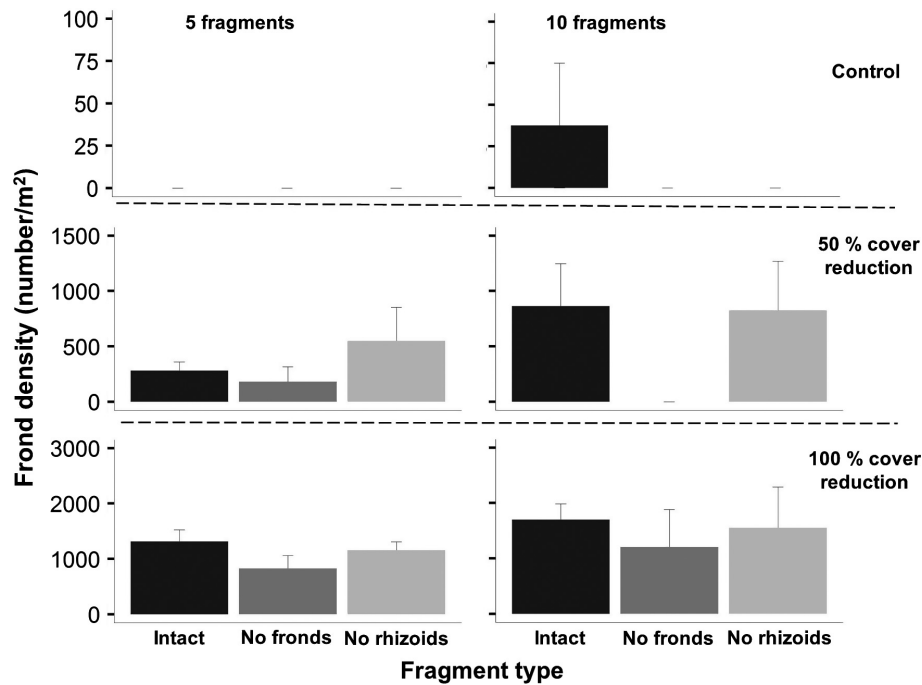


FIG. 3. Density of fronds of *Caulerpa cylindracea* (number/m<sup>2</sup>) under different combinations of disturbance intensity, propagule pressure and propagule quality. Data are means ± Standard Error. Differences in the y-axis scale should be considered when comparing disturbance intensity levels.

DISCUSSION

While there is increasing acknowledgement that invasion success is regulated by multiple factors, experimental tests including combinations of factors are still relatively uncommon (but see Thomsen et al. 2006, Clark and Johnston 2009, Estrada et al. 2016, Byun et al. 2017). Here, we show that disturbance to native canopies, propagule quality and number influence invasion success. As predicted, disturbance had the strongest effect on invasion success, with seaweed cover, biomass, total stolon length and frond density per plot increasing with growing intensity of disturbance to seagrass canopies. In addition, propagule quality had a stronger influence on fragment biomass and traits compared

to propagule number. The effects of the individual factors were independent and did not interact to determine fragment establishment.

Increasing reductions in the cover of the seagrass *P. oceanica* enhanced the establishment of *C. cylindracea*. This supports previous studies showing positive effects of disturbance to native assemblages on invasion success via increased resource availability (Burke and Grime 1996, Davis et al. 2000, Bulleri et al. 2010, Ceccherelli et al. 2014). Although we did not investigate how disturbance of *P. oceanica* canopy promoted the establishment of *C. cylindracea*, the main mechanism was likely an increase in access to light (Marin-Guirao et al. 2015). Light levels can be reduced by 60–89% in intact seagrass beds compared to outside, potentially limiting

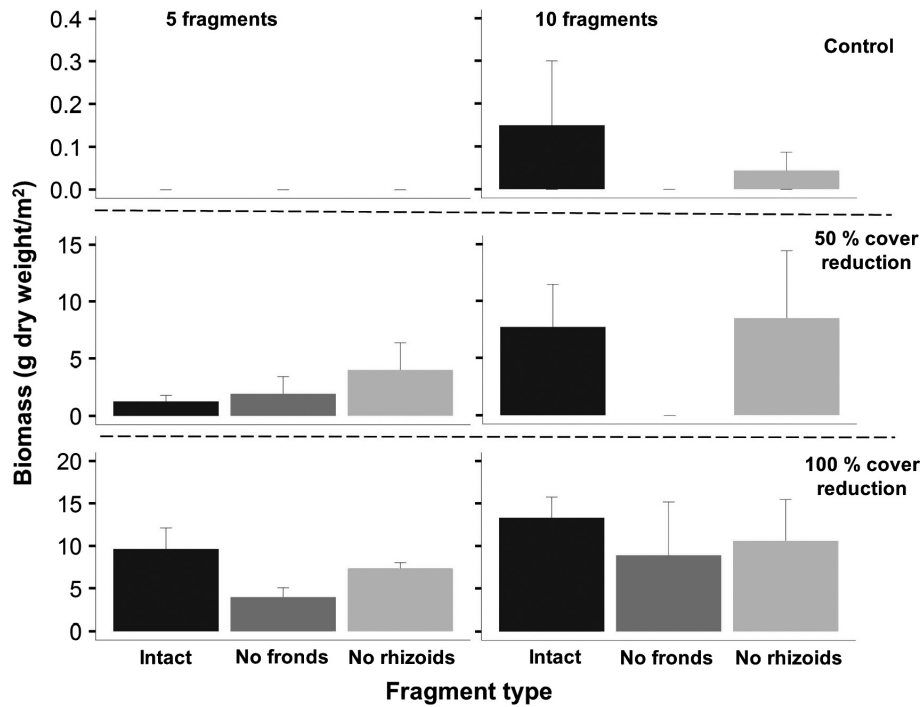


FIG. 4. Biomass of *Caulerpa cylindracea* ( $\text{g/m}^2$ ) under different combinations of disturbance intensity, propagule pressure and propagule quality. Data are means  $\pm$  Standard Error. Differences in the y-axis scale should be considered when comparing disturbance intensity levels.

TABLE 2. ANOVA on the effects of disturbance intensity (*D*), propagule pressure (*P*) and propagule quality (*Q*) on frond density, mean frond length, total stolon length, rhizoid density and biomass of *Caulerpa cylindracea*. Post-hoc Tukey's HSD tests are reported when the main analysis showed significant effects of *D*, *Q* or their interaction.

Source of variation	df	Frond density		Mean frond length		Total stolon length		Rhizoid density		Biomass	
		MS	F	MS	F	MS	F	MS	F	MS	F
<i>D</i>	2	16368.7	27.871***	12.125	47.925***	104601	21.086***	35212.0	16.638***	1.746	39.682***
<i>P</i>	1	1250	2.128	0.001	0.004	23875	4.181*	5425.0	2.563	0.071	1.614
<i>Q</i>	2	1320.9	2.247	1.794	7.091**	13461	2.714	4150.0	1.961	0.191	4.341*
<i>D</i> $\times$ <i>P</i>	2	339.5	0.578	0.030	0.119	6323	1.275	1803.0	0.852	0.009	0.205
<i>D</i> $\times$ <i>Q</i>	4	384.9	0.655	0.884	3.494*	3956	0.797	1303.0	0.616	0.058	1.312
<i>P</i> $\times$ <i>Q</i>	2	174.9	0.300	0.188	0.743	2874	0.579	216.0	0.102	0.046	1.045
<i>D</i> $\times$ <i>P</i> $\times$ <i>Q</i>	4	148.9	0.254	0.414	1.636	2828	0.570	682.0	0.322	0.044	1
Residual	53	587.3		0.253		4960.6		2116.3		0.044	
Transformation		None		None		None		None		Square root	
Cochran's test		<i>P</i> < 0.05		<i>P</i> = 0.120		<i>P</i> < 0.05		<i>P</i> < 0.05		<i>P</i> = 0.120	

post-hoc Tukey's HSD tests

Frond density	<i>D</i>	100% > 50% > Control
Mean frond length	<i>D</i> $\times$ <i>Q</i>	Control: Intact = no rhizoids = no fronds 50%: Intact = no rhizoids > no fronds 100%: Intact = no rhizoids = no fronds
Total stolon length	<i>D</i>	100% > 50% > Control
Rhizoid density	<i>D</i>	100% > 50%; 100% > Control
Biomass	<i>D</i>	100% > 50% > Control
	<i>Q</i>	Intact = no rhizoids > no fronds

\**P* < 0.05; \*\**P* < 0.01; \*\*\**P* < 0.001.

the growth of *C. cylindracea* (Marin-Guirao et al. 2015). In fact, in our study, a 50% canopy reduction was sufficient to increase the cover, biomass and frond density of *C. cylindracea* to values observed in the 100% canopy removal

treatment. Thus, invasion of native marine macrophytes may happen at lower levels of disturbance than often considered, highlighting the limitations of marine studies that have typically considered removal of the entire native canopy vs.

non-removal (Valentine and Johnson 2003, Britton-Simmons and Abbott 2008, Bulleri et al. 2010). Understanding critical levels, or thresholds, at which disturbance facilitates invasion is clearly an important avenue for future research. This is a pressing issue for *C. cylindracea* given the current declining trends of *P. oceanica* seagrass meadows in the Mediterranean Sea (Marbà et al. 2014).

General theory and empirical research provide compelling evidence of the role of species' traits in regulating establishment success (Stearns 1992, Marshall et al. 2006). Although rarely studied in an invasion context, fragment quality had strong consequences for cover and total biomass measured at the end of the experiment. In accordance with the results of Bulleri et al. (2018), fragments without fronds consistently performed worst when compared to fragments with fronds (both intact and without rhizoids). This was somewhat surprising given that the rhizoids of other invasive *Caulerpa* spp. perform vital functions such as fixing N<sub>2</sub>, which in turns promotes organic matter turnover and nutrient acquisition (Chisholm and Moulin 2003). The strong effect of the presence/absence of fronds suggests that light was, again, the likely limiting resource for *C. cylindracea*.

The stolon and fronds of *C. cylindracea* contain photosynthetic pigments such as chlorophyll *a*, siphonoxanthin and siphonein (Raniello et al. 2004). *C. cylindracea* fragments initially deprived of fronds had lower total stolon length and biomass, but, by the end of the experiment, they were able to re-grow fronds to densities matching those found in other types of fragments. Since this seaweed is coenocytic, the removal of fronds could result in a rapid reallocation of energy to increase their re-growth at expense of the lateral expansion, as found for several other *Caulerpa* spp. (Collado-Vides and Robledo 1999). The lack of differences in rhizoid density between fragments that had their rhizoids removed and intact ones at the end of the experiment suggests that there is also a reallocation of energy to rhizoid re-growth. Because of the small loss of biomass associated with rhizoid removal (Capiomont et al. 2005), new rhizoids may be quickly generated without major consequences on final biomass and total stolon length (Bulleri et al. 2018).

Increasing fragment number, although having weaker effects than disturbance and fragment quality on seaweed establishment, increased the final percent cover of *C. cylindracea*. However, a doubling from 5 to 10 fragments/quadrat did not result in a doubling of the percent cover or biomass of fragments in plots. This might be a consequence of intraspecific competition among fragments at the highest fragment number treatment. Competition for light among fragments is unlikely to explain this pattern, as *C. cylindracea* can be found up to 70 m deep at high densities (Klein and Verlaque 2008). At higher densities, fragments may be competing for other resources such as nutrient supply. Intra-specific competition as a consequence of nutrient limitation among early growth stages has been documented in invasive terrestrial plants (Blank 2010) and marine macroalgae (Steen 2003, Steen and Scrosati 2004). We suggest that intraspecific competition among invasive propagules may have important, but currently underestimated, consequences for the establishment and demography of non-native plants.

Previous studies have clearly demonstrated that different factors (e.g., disturbance and propagule pressure) interact to determine invasion success (D'Antonio et al. 2001, Thomsen et al. 2006, Britton-Simmons and Abbott 2008). In our experiment, the effects of canopy disturbance, fragment quality and number were independent. Our prediction that the success of low quality fragments (fragments without fronds) would increase with increasing disturbance levels was supported, as no-frond fragments could establish only in total canopy removal plots. In contrast, the prediction that high quality fragments (i.e., intact) would be successful across all disturbance regimes, independently of their number was not supported; in fact, high and intermediate quality fragments persisted under intact seagrass canopy only when transplanted in large numbers. This suggests subtle interactions among disturbance, propagule quality and number may occur, but were not detected in our analyses because of the low values of cover and biomass achieved by *C. cylindracea* under full canopies. *P*-values close to significance for interactions between disturbance and either propagule quality or propagule pressure on seaweed cover (see Table 1) support the proposition that the cover of *C. cylindracea*, at the peak of the growing season (when our experiment was conducted), could be influenced by the characteristics of both propagules and the recipient habitat.

In summary, our results suggest a stronger role of propagule quality compared to propagule number in the establishment of *C. cylindracea*. For fast-growing, asexually reproducing invasive species, propagule traits enhancing the ability to acquire the specific resources freed by disturbance - in our case, light - appear key for their successful establishment and spread. Under these circumstances, the traits of propagules conferring greater establishment ability likely vary among disturbances that free different resources (i.e., beneficial traits may be disturbance-specific). Our results may also reconcile contrasting results of the effects of disturbance on invasion success (Moles et al. 2012): disturbance may facilitate non-native establishment only when propagules possess the traits necessary to acquire freed resources. By contrast, weak effects of resource release or input can be expected when propagules are unable to exploit them, independently of their abundance. Under these circumstances, assessing the matching between the quality or type of resource made available through disturbance and the characteristics of non-native propagules may greatly enhance our ability to forecast invasion success in environments increasingly exposed to human perturbations. More broadly, a functional approach, based on resource-exploitation traits of propagules (i.e., fragments, larvae, spores or adults), might allow identifying non-native species or morpho-types within species more likely to benefit from a specific disturbance regime.

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## LITERATURE CITED

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