

Effects of mean intensity and temporal variability of disturbance on the invasion of *Caulerpa racemosa* var. *cylindracea* (Caulerpales) in rock pools

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Abstract Disturbance is a key factor influencing the invasibility of habitats and assemblages. This relationship was extensively studied in terrestrial systems, but it was scarcely tested in the marine environment. We investigated experimentally the interactive effects of changes in the intensity and temporal variability of mechanical disturbance by boulders on invasion dynamics of the green alga *Caulerpa racemosa* var. *cylindracea* in littoral rock pools. We tested the hypothesis that the success of invasion of *C. racemosa* would be (1) greater under large than under low intensity of disturbance, (2) greater under large than under low temporal variability of disturbance and that (3) interactive effects could also occur, with variability of disturbance magnifying the effects of intensity. *C. racemosa* was virtually absent in pools maintained under high intensity of disturbance, independently of temporal variability. High intensity of disturbance was also associated with lower density and length of fronds and thinner diameter of the stolons of the alga. The total number of native taxa and the abundance of

encrusting coralline algae increased under high intensity of disturbance. Differently, turf-forming algae were positively affected by temporal variability of disturbance, while canopy-forming algae did not respond to experimental treatments. Our results suggest a direct negative effect of the most severe experimental conditions on the spread of *C. racemosa* in rock pools. This likely overwhelmed likely concomitant positive and negative effects mediated by resident organisms. The results of this study help anticipating invasion dynamics of *C. racemosa* in rock pools under climate change scenarios, in which both intensity and temporal variability of extreme meteorological events are predicted to increase.

Keywords *Caulerpa racemosa* var. *cylindracea* · Disturbance · Invasion · Mediterranean Sea · Mean intensity · Rock pools · Temporal variability

Introduction

The invasion of habitats by non-native species is a global phenomenon with relevant ecological, economic, and social consequences (Williamson 1999; Pimental et al. 2000; Bax et al. 2003). Invasive species cause reductions in the number and abundance of native species, alterations of the structure of native habitats and modifications of ecosystem processes (Grosholz 2002). This makes invasive species a main cause of decreasing biodiversity, second only

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to habitat loss (Vitousek et al. 1997; Mack et al. 2000).

One of the main issues in invasion ecology is the understanding of processes and basic mechanisms driving the susceptibility of ecosystems and native assemblages to invasions (Lonsdale 1999; Stohlgren et al. 1999; Williamson 1999). The traditional approach to understand invasions focused on properties of the organisms themselves, including traits of both the potentially invading species and the native species that are subject to this pressure (Baker 1974; Newsome and Noble 1986; Daehler and Carino 2000; Kolar and Lodge 2001; Shea and Chesson 2002). However, a complete understanding of the invasion process requires assessing the environmental conditions contributing to the success of invaders (Shea and Chesson 2002).

An important factor influencing the invasibility of habitats and assemblages is the degree of disturbance to which they are exposed (Elton 1958). Studies conducted in a variety of systems have led to the generality that high levels of disturbance may promote invasions through increasing the availability of resources, such as space, light and nutrients, and by reducing competition with native species (Burke and Grime 1996; Davis et al. 2000; Prieur-Richard et al. 2000). The timing of disturbance with respect to periods of reproduction and recruitment of organisms and the availability of free space can also have drastic effects on the ability of populations to colonize (Kennelly and Larkum 1983; Dayton et al. 1984).

The question of whether disturbance affects invasion dynamics, although considerably debated in terrestrial systems (Hobbs and Atkins 1988; D'Antonio and Vitousek 1992; Burke and Grime 1996; Lake and Leishman 2004), still needs to be addressed experimentally in marine systems (but see Clark and Johnston 2005), as the majority of previous studies focused on diversity-invasion relationships (Stachowicz et al. 2002; Arenas et al. 2006; Britton-Simmons 2006; Sánchez and Fernández 2006) or on the life-history traits of resident and invading species that may be relevant for the invasion process (Strong et al. 1984; Cronk and Fuller 1995; Rhymer and Simberloff 1996; Stachowicz et al. 1999; Scheibling and Gagnon 2006). Recent theoretical and experimental studies have specifically investigated the interactive effects of the mean intensity (the physical force of events per unit of area and time) and the temporal

variance (the distribution of events over the temporal scale considered) of disturbance on rocky shore organisms (Benedetti-Cecchi 2003; Bertocci et al. 2005, 2007; Benedetti-Cecchi et al. 2006), but these issues have not yet been related to invasion dynamics.

The Mediterranean Sea, with more than 80 introduced species, is the sea basin that harbours the greatest number of introduced macroalgae at the global scale (Boudouresque and Verlaque 2002; Klein et al. 2005). Since the early 1990s, the green alga *Caulerpa racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman et Boudouresque (hereafter, *C. racemosa*) is undergoing a dramatic spread compared to other introduced macroalgae in Europe (Klein and Verlaque 2008). This represents one of the most serious invasive events ever documented, with invaded areas occurring throughout almost the whole basin (Piazzi et al. 1994, 2005a; Modena et al. 2000). *C. racemosa* is able to colonize different substrata, such as rock, sand and cobbles, at depth ranging from 0 to 40 m where turfs, erect algae or seagrasses are present (Piazzi and Balata 2009). Previous studies on the ecology and physiology of *C. racemosa* have focused on subtidal populations, showing a period of maximal growth during the warm season and a sharp decrease during the coldest months, with persistent prostrate stolons enabling the quick recovery of erect fronds the following season (Ceccherelli et al. 2000; Balata et al. 2004; Cavas and Yurdakoc 2005; Piazzi et al. 2005b; Piazzi and Ceccherelli 2006). In the last years, this species has started to spread also into intertidal rock pools located along the Tuscany coast in the north-west Mediterranean (M. Incera et al., personal observation).

The rocky intertidal is a highly spatially and temporally variable environment, with a gradient of increasing harshness for marine species from the lower to the upper limits. Within this zone, littoral rock pools provide refuge habitats for a variety of marine organisms during low-water periods due to tidal cycles (Underwood 1980; Dethier 1982, 1984; Underwood and Jernakoff 1984; Astles 1993) or to calm sea associated with high barometric pressure, such as in the Mediterranean Sea. Nevertheless, organisms inhabiting rock pools are subject to stressful environmental conditions during these periods, with large fluctuations over short temporal scales in physical and chemical variables, such as temperature, salinity, dissolved oxygen and pH (Huggett and Griffiths 1986). Rock pools may allow *C. racemosa*

to invade the intertidal habitat, but also represent marginal systems where its establishment and persistence may depend on direct and indirect effects of disturbance and on the influx of propagules from source populations in the subtidal zone.

In this study, we investigated experimentally the relationship between patterns of invasion of *C. racemosa* inside rock pools and changes in the intensity and temporal variability of disturbance due to the overturning of boulders by waves. Although *C. racemosa* was sparse in the rock pools at the beginning of the study, the possibility that this alga can establish dense populations in this habitat is not remote, as it has been documented for other shallow habitats in the same area (Piazzi et al. 2005a). In fact, successful non-indigenous species frequently exhibit a lag phase, during which populations persist at low numbers before rapidly increasing (Kowarik 1995; Crooks and Soulé 1999). Our rock pools, therefore, provided a unique opportunity to examine the effects of disturbance on the spread of an invasive species as it became established in a new habitat—i.e., at the onset of the invasion process. Specifically, we hypothesized that the success of invasion of *C. racemosa* would be (1) greater under high than under low intensity of disturbance, (2) greater under large than under low temporal variability of disturbance and that (3) interactive effects could also occur, with variability of disturbance magnifying the effects of intensity. Examining the effects of changes in disturbance regimes on invasion is important in the context of climate change, where several models predict shifts in both the mean intensity and temporal variability of climate events (Allen et al. 2000; Benestad 2003), including storms (Michener et al. 1997; Muller and Stone 2001).

Materials and methods

The study site

The study was conducted in rock pools distributed along the shore of Calafuria, Italy (NW Mediterranean Sea, 43°30'N, 10°20'E), between September 2005 and October 2006.

This habitat is naturally exposed to mechanical disturbance determined by the overturning of boulders by waves, which can partially or completely

displace resident algae and invertebrates, creating patches of bare substrate (Dethier 1984). Assemblages were composed of stands of canopy-forming species such as *Cystoseira brachycarpa* var. *balearica* (Sauvageau) Giaccone, *Cystoseira compressa* (Esper) Gerloff & Nizamuddin and *Cystoseira crinita* Bory, interspersed among patches of turf-forming algae such as *Corallina elongata* Ellis and Solander, *Stypocaulon scoparium* (Linnaeus) Kützinger, *Padina pavonica* (Linnaeus) Thivy and encrusting corallines, mainly belonging to the genus *Lithothamnion*. Invertebrates included the barnacle *Balanus perforatus* Bruguière, the tube-forming gastropod *Vermetus triquetrus* Bivona Ant., spirorbids and chitons. Further descriptions of these assemblages are reported elsewhere (Benedetti-Cecchi and Cinelli 1992a, b).

Experimental design

A total of 24 rock pools were selected at random along a stretch of coast about 2 km long with a similar exposure to swell. These pools ranged in size from 1.4 to 8 m², had a mean depth of about 40 cm and all supported algal assemblages dominated by canopy-forming species, turf-forming species and encrusting coralline algae, as described above. The scouring of the substratum by boulders driven by wave action during storms is a major source of disturbance for assemblages in these pools. We quantified the number, size and weight of boulders per unit area in these pools in a parallel study (unpublished data) and used these values as a surrogate measure of the intensity of disturbance to which assemblages were exposed. The median weight of boulders in the pools was 8 kg m⁻², with the size of most boulders in the range 5,000–12,000 cm³.

The intensity and temporal variability of mechanical disturbance were manipulated in an asymmetrical design. This included three control pools where boulders were not manipulated (control), three pools where boulders were continuously removed (removal), and three pools assigned at random to each combination of the following treatments: (1) intensity (two levels: high and low) and (2) temporal variability of disturbance (three levels: no variability due to the constant presence of boulders, low and high variability). Caution was made in interspersing treatments among pools differing for the presence of

C. racemosa at the beginning of the experiment, provided that pools with and without this alga were included among the three pools in each experimental condition. The two levels of intensity were chosen on the basis of the median weight of boulders observed in the pools: we used 8 and 16 kg m⁻² of boulders for low (LI) and high (HI) intensity, respectively. Manipulated boulders were taken from the intertidal habitat around the pools and were in the same range of sizes of those found naturally in the pools. These boulders were free of any macroscopic organism, likely due to their frequent overturning by waves along the shore. The condition of no variability of disturbance was obtained by maintaining boulders continuously (C) inside rock pools. The conditions of low (LV) and high (HV) temporal variability of disturbance were produced by alternating periods in which pools had boulders with periods in which boulders were removed. These periods were distributed almost regularly in the LV treatment, resulting in a variance for the intervals of time between successive disturbances of 0.5 months² (bad weather prevented a perfectly regular distribution of events in time that would have resulted in zero variance). Periods of disturbance were distributed heterogeneously during the course of the study in the HV treatment, resulting in a temporal variance of 6 months² (Fig. 1). Total duration of disturbance was kept constant between LV and HV treatments (6 out of the 12 months in which the experiment run). In the C treatment, where pools were disturbed for the whole period of the experiment, the weight of boulders was halved to 4 and 8 kg m⁻² for the LI and HI treatments, respectively. Thus, intensity of disturbance was the same for the C, LV and HV treatments over the course of the experiment.

Boulders displaced by storms were replaced as soon as environmental conditions enabled a safe access to the shore. It is worth noting that disturbance by boulders was necessarily associated with a rough sea. Therefore, the effectiveness of our treatments depended on the number of storms that occurred during the course of the study. Data on storms at the study site were collected from the LaMMA (Laboratorio di Monitoraggio e Modellistica Ambientale della Regione Toscana: <http://www.lamma.rete.toscana.it/>) meteorological station located in Livorno. Rough sea events characterized by on-shore winds (between 180 and 360° for the study site) with daily average speed

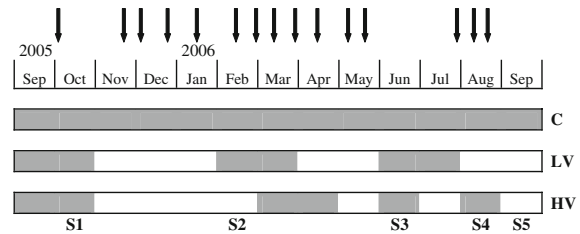


Fig 1 Schematic representation of the distribution of events of disturbance over the course of the experiment for each level of temporal variability. *Black and white blocks* represent periods in which disturbance was present or absent, respectively. The full experimental design includes two levels of intensity crossed with each level of variability, with three replicate rock pools nested in each condition, three pools subject to continuous disturbance and three unmanipulated pools. S1–S5 are the dates of sampling. *C* continuous disturbance, *LV* low variability, *HV* high variability. *Black arrows* indicate storm events enough to move boulders in pools (see details in the text)

larger than 5 m/s (corresponding to waves at least 1 m in height, according to the Beaufort scale) were considered strong enough to move the boulders that were placed into the pools. A total of 15 storms with these characteristics occurred during the course of the study, 6 of which coincided with the presence of boulders in pools allocated to each of the different levels of temporal variability of disturbance (Fig. 1). Therefore, the conditions for disturbance to operate were real in our experiment and comparable across treatments. The only exception concerned the C treatment where the continuous presence of boulders exposed rock pools to more frequent disturbances. Therefore, any difference between this and the other treatments must be interpreted with caution.

Sampling and statistical analyses

Assemblages were sampled five times during the experiment. At each date of sampling, the interval of time since the last disturbance necessarily differed among levels of temporal variability. To avoid confounding effects of treatments with differences in elapsed time since disturbance, sampling dates were chosen so that the mean interval of time since the last event of disturbance was constant across treatments, with the obvious exception of pools disturbed continuously (Fig. 1).

Sampling was done in five replicate quadrates of 256 cm² interspersed at random in each rock pool

at each date. A plastic frame of 16×16 cm divided into 64 sub-quadrates of 2×2 cm was used to obtain visual estimates of the abundance of *C. racemosa*. This was calculated by assigning to the cover of the alga in each sub-quadrate a score ranging from 0 to 4, then adding up the 16 estimates and expressing final values as percentages (Dethier et al. 1993). We also sampled the density and length of fronds and the diameter of stolons. Density was quantified by counting the number of fronds in three sub-quadrates selected at random within each sampling unit. Three measures of the length of fronds and of the diameter of stolons were taken at random in each 16×16 cm quadrat with a plastic calliper.

In order to evaluate possible indirect effects of disturbance on invasion through changes in native assemblages, the total number of native taxa (a surrogate measure of species diversity) and the percentage cover of the three most abundant morphological groups of algae (encrusting coralline, turf-forming and canopy-forming algae) identified in rock pools were measured in each 16×16 cm quadrat at each date of sampling.

Statistical analyses were done on data averaged across the five quadrates in each pool at each date, so that pools provided the replicate units in the experiment. Data were analysed with Population-Averaged Generalized Estimating Equations (PA-GEEs), an extension of Generalized Linear Models (GLMs) for correlated data (Liang and Zeger 1986; Quinn and Keough 2002). This procedure provides estimates of model parameters and standard errors that take into account correlated observations (Burton et al. 1998). PA-GEEs were needed in this work for two reasons. First, our hypotheses concerned the entire duration of the experiment and not single dates of sampling. Second, each experimental unit (rock pool) was sampled repeatedly through time and, although we used different quadrats at each time, data might have been serially correlated. PA-GEEs were run using the “geeglm” procedure in the R program, version R2.6.1, specifying a link function and an error structure for the residuals. We used a first order autoregressive model AR(1) in all the analyses assuming a time dependence for each rock pool. We note that the procedure is robust to misspecification of the correlation structure (Hardin and Hilbe 2003). For data expressed as percentage

cover, density of fronds and size (length of fronds and diameter of stolons) of *C. racemosa*, we assumed a Gaussian distribution of the error terms and we used an identity link to relate the linear predictor with expected values of the response variable. A logit function and binomial errors were used to model presence/absence data for *C. racemosa*.

Tests of hypotheses were based on contrasts and compared the treatment where boulders were continuously removed versus all other treatments where boulders were present, including control, in first place. This text examined the effect of removing disturbance. Effects of experimental disturbance were examined by contrasting treatments where boulders were manipulated with control. Finally, the effects of intensity and temporal variability of disturbance were tested using the LV treatment for reference. The C versus LV contrast examined the effect of two extreme situations with (nearly) zero variance, a constant versus a regularly fluctuating environment. The HV versus LV contrast examined the effect of an increase of temporal variability of disturbance, as predicted by models of climate change. The full analyses included tests of interactions of each of these contrasts with intensity of disturbance, using the LI treatment for reference. Lack of convergence prevented the use of the full model on presence/absence data of *C. racemosa*, so the analysis on this variable was based on a reduced model that omitted the C versus LV contrast and its interaction with intensity of disturbance.

Plots of residuals were examined after each analysis to check for normality and homogeneity of variances. Some degree of variance heterogeneity was observed for all the response variables associated with *C. racemosa*. The outcomes of these analyses were interpreted using a conservative value for Type I errors of $\alpha = 0.01$. Assumptions were met for the abundances of algal groups and the conventional significance level of $\alpha = 0.05$ was used in this case.

Results

Caulerpa racemosa

Intensity of disturbance significantly affected all response variables associated with *C. racemosa*

(Table 1). The occurrence of this alga was significantly reduced in control compared to treated pools and in HI compared to LI treatments (Table 1). Similarly, the density and length of fronds and the diameter of stolons of the alga were significantly lower in HI than LI treatments (Table 1; Fig. 2a–c, respectively). Temporal variability of disturbance, in contrast, had no effect on *C. racemosa* either as a main effect or in interaction with other factors (Table 1).

Native organisms

Intensity of disturbance affected the number of taxa and the abundance of encrusting coralline algae independently of temporal variability (Table 2). On average, both response variables were larger under high intensity of disturbance (Fig. 3a, b).

Temporal variability of disturbance had a significant positive effect on the percentage cover of turf-forming algae, under both levels of intensity

Table 1 Results of PA-GEEs examining the effects of intensity and temporal variability of disturbance on the invasion success of *C. racemosa*

Contrasts	Presence/absence		Density of fronds		Length of fronds		Diameter of stolons	
	<i>E</i>	<i>SE</i>	<i>E</i>	<i>SE</i>	<i>E</i>	<i>SE</i>	<i>E</i>	<i>SE</i>
Intercept	−0.90***	0.27	0.55***	0.14	1.48***	0.38	0.10***	0.02
Removal vs. others	−0.11	0.12	−0.02	0.07	0.05	0.10	−0.00	0.01
Control vs. treatments	−0.24*	0.11	−0.02	0.04	−0.04	0.16	−0.01	0.01
HI vs. LI = I	−1.14**	0.31	−0.48**	0.15	−1.31**	0.47	−0.07**	0.03
HV vs. LV	0.15	0.38	0.15	0.20	0.08	0.55	−0.02	0.03
C vs. LV			−0.07	0.20	−0.21	0.50	0.01	0.03
I × HV vs. LV	−0.56	0.38	−0.18	0.20	−0.26	0.55	0.00	0.03
I × C vs. LV			0.10	0.20	0.43	0.50	0.03	0.16
Correlation parameter	0.09	0.07	0.33	0.10	0.48	0.10	0.15	0.17
Scale parameter	0.99	0.32	1.08	0.33	6.60	2.38	0.04	0.01

E estimate, *SE* standard error, *HI* high intensity, *LI* low intensity, *HV* high variability, *LV* low variability, *C* continuous disturbance

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Fig 2 Mean (+SE, $n = 3$) density (a) and length (b) of fronds and diameter of stolons (c) of *C. racemosa* over five dates of sampling. *HI* high Intensity, *LI* low Intensity

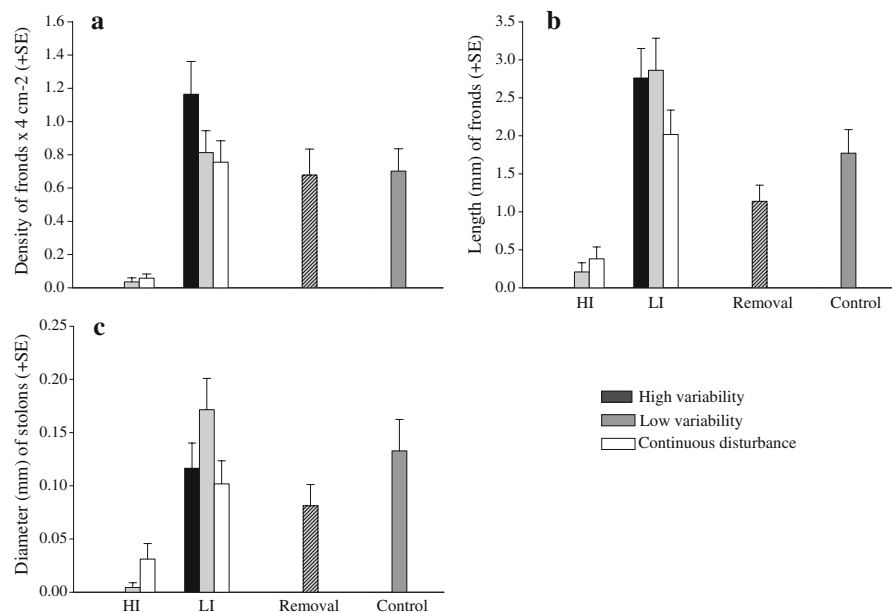
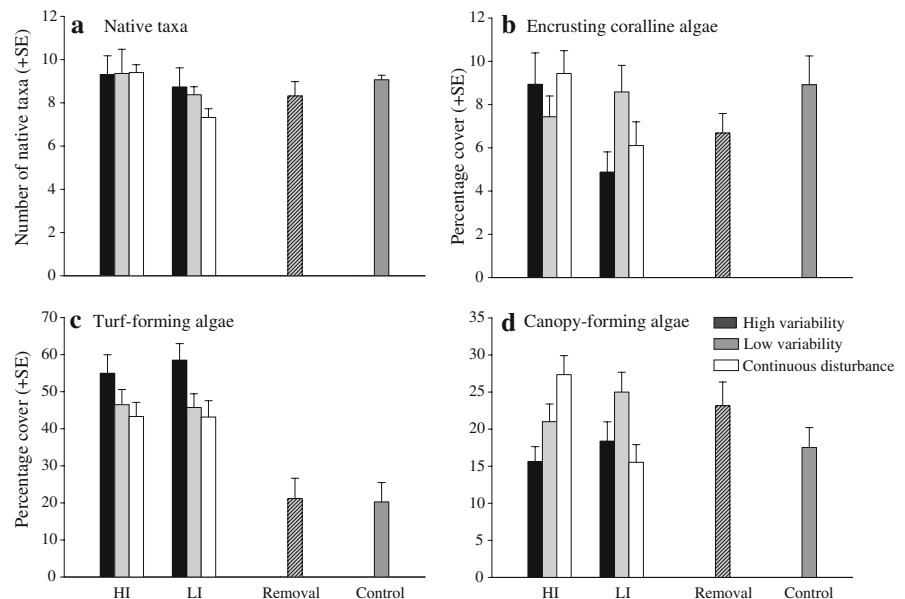


Table 2 Results of PA-GEEs examining the effects of intensity and temporal variability of disturbance on native assemblages

Contrasts	Number of native taxa		Encrusting corallines		Turf-forming algae		Canopy-forming algae	
	<i>E</i>	SE	<i>E</i>	SE	<i>E</i>	SE	<i>E</i>	SE
Intercept	8.72***	0.20	8.65***	0.54	49.70***	1.23	20.15***	2.90
Removal vs. others	0.05	0.08	0.09	0.37	0.36	0.42	−0.23	2.11
Control vs. treatments	−0.04	0.04	−0.26	0.18	−0.71*	0.31	0.40	0.63
HI vs. LI = I	0.60*	0.24	1.05*	0.50	−0.27	1.53	0.73	2.62
HV vs. LV	0.26	0.37	−0.73	0.67	7.37**	2.50	−4.19	3.44
C vs. LV	−0.39	0.27	−0.22	0.77	−5.89**	2.13	1.78	4.20
I × HV vs. LV	−0.29	0.37	0.94	0.67	−2.32	2.50	−1.07	3.44
I × C vs. LV	0.40	0.27	0.64	0.77	0.14	2.13	4.76	4.20
Correlation parameter	0.12	0.09	−0.12	0.08	0.05	0.07	0.64	0.07
Scale parameter	2.99	0.45	53.23	8.03	292.80	27.90	245.95	47.3

Symbols and abbreviations as in Table 1

Fig 3 Mean (+SE, $n = 3$) number of native taxa (a) and percentage cover of encrusting coralline (b), turf-forming (c) and canopy-forming (d) algae over five dates of sampling. HI high intensity, LI low intensity



(Table 2; Fig. 3c). In particular, a constant regime of disturbance significantly reduced the cover of these algae compared to the variable regime (the C vs. LV contrast in Table 2). Algal turfs were also less abundant in the unmanipulated condition than, on average, in conditions where boulders were manipulated experimentally (Table 2; Fig. 3c).

There was no significant effect of treatments on the percentage cover of canopy-forming algae (Table 2). These algae, however, tended to decrease in abundance across C, LV and HV treatments under

high intensity of disturbance, whilst under low intensity they attained the largest abundance in the LV treatment (Fig. 3d).

Discussion

The experimental results indicated that physical disturbance by boulders had significant effects both on the introduced alga *C. racemosa* and on the resident algal assemblages. Our prediction that high

intensity of disturbance combined with high temporal variability would increase the invasibility of resident assemblages was not supported by the results. In contrast, we observed that both the abundance and size of this alga were drastically reduced in heavily disturbed pools compared to the other treatments. Temporal variability of disturbance was, however, an important driver of the cover of turf-forming algae, the dominant organisms in the pools.

Our findings contrast with theoretical (Pausas et al. 2006) and experimental (Burke and Grime 1996; Lake and Leishman 2004; Clark and Johnston 2005; Kneitel and Perrault 2006) studies indicating that disturbance commonly facilitates the establishment of non-native species through direct and indirect mechanisms (Davis et al. 2000; Davis and Pelsor 2001; Shea and Chesson 2002). Williams and Smith (2007), in particular, have recently reviewed more than 400 global introduction events of seaweeds. Although only four studies reported negative effects of disturbance on invasion, these examples highlighted the importance of indirect effects in regulating the establishment and spread of non-indigenous species. Piazzini et al. (2003) indicated that disturbance can hinder invasion of *C. racemosa* by removing facilitators like turf-forming algae. These algae, in fact, create a complex three-dimensional habitat that can entrap the fragments and anchor the stolons of *C. racemosa* (Ceccherelli et al. 2002). Similarly, canopy algae can offer a favourable understory habitat for invaders that require a low light and wetter environment (Reed and Foster 1984; Duggins et al. 1990; Mc Cook and Chapman 1991), so that any disturbance that affects the canopy has also negative effects on the introduced species. This was the case for the recruitment of *Sargassum muticum*, which decreased upon removal of the native canopy-forming alga *Bifurcaria bifurcata* (Sánchez and Fernández 2006). A similar example involved interactions between mussels and the introduced alga *Codium fragile* ssp. *tomentosoides* in the north Adriatic Sea (Bulleri and Airolidi 2005). Mussels facilitated invasion by reducing the dislodgement of the alga by waves at exposed sites. The experimental removal of mussels, mimicking human harvesting during the summer, had negative effects on the introduced alga. Finally, indirect interactions can affect invasion also through trophic interactions, as it was shown by Sala and Boudouresque (1997): the exclusion of herbivorous fish determined a reduced invasion by the red alga

Asparagopsis armata due to the consequent dominance of the substratum by fleshy erect algae.

Our results can be mainly explained by direct effects of disturbance on patterns of invasion of *C. racemosa*. A possible mechanism could be the prevention, through mechanical destruction, of the establishment of propagules or fragments of *C. racemosa* under intense disturbance. The invasion abilities of non-indigenous species are, in fact, highly dependent on the number of propagules introduced and on the frequency of introduction events, i.e., the propagule pressure (Williamson 1999; Grevstad 1999; Lonsdale 1999; Kolar and Lodge 2001; Lockwood et al. 2005; Drake and Lodge 2006). Similarly to what was suggested for Mediterranean French coasts, where strong wave action, combined with sediment scouring, prevented the establishment of *C. racemosa* at depths between 0 and 10 m (Ruitton et al. 2005a), our result can be a consequence of the absence of efficient anchoring structures in the dispersal stages of *C. racemosa*, which, in contrast, attaches firmly to the substratum with rhizoids as an adult. The increased abundance of algae of the same genus in disturbed patches of bare substratum reported previously was, in fact, due to lateral growth and expansion from adjacent areas, rather than to the immigration of new propagules (Stafford and Bell 2006).

In addition to indirect effects mediated by boulders, storms could have affected *C. racemosa* directly in the experimental pools. The direct effect of wave action is likely to contribute to the disappearance of the erect fronds of *C. racemosa* from subtidal habitats during the winter, when storms are more frequent and intense (Balata et al. 2004; Ruitton et al. 2005b). Although this effect might have operated also in our rock pools, waves alone were likely to have much less impact than wave-born boulders. As shown by Shanks and Wright (1986), rocks driven by waves are far more destructive than waves alone when impinging on intertidal assemblages.

Processes other than disturbance were unlikely to account for the observed results. By allocating replicated pools randomly across treatments, our experimental design did not introduce any bias with respect to potential confounding factors such as differences in the physical characteristics among pools (see “Materials and methods”). Analogously, pools subjected to high and low intensity of disturbance were similar in size (6.43 ± 1.63 and

$7.62 \pm 4.09 \text{ m}^2$, respectively), depth (46.46 ± 5.62 and $35.50 \pm 7.63 \text{ cm}$, respectively) and distance from the sea (6.88 ± 2.53 and $5.50 \pm 2.75 \text{ m}$, respectively), suggesting that the differences we found in abundance and size of *C. racemosa* among these treatments were not due to differences in the physical characteristics of the pools. Instead, our results provided robust evidence of the importance of the mechanical disturbance of boulders as a mechanism limiting the ability of *C. racemosa* to spread in rock-pools.

The direct negative effect of high intensity of disturbance on *C. racemosa* might have offset any positive indirect effect resulting from the release of resources (e.g., new space for colonization) or from facilitative influences by resident taxa such as turf-forming algae. It has been shown, in fact, that the success of invasion of *C. racemosa* was greater in algal turfs than in habitats dominated by encrusting coralline algae (Ceccherelli et al. 2002), likely due to the stabilizing effect of turf-forming algae on fragments and stolons of *C. racemosa*. Such a mechanism was supported by the experimental evidence that plastic mimics reproducing the three-dimensional structure of algal assemblages and intact native turfs are comparably more effective in facilitating the spread of *C. racemosa* relatively to barren habitats (Bulleri and Benedetti-Cecchi 2008). The relative large abundances of both *C. racemosa* and algal turfs observed in rock pools maintained at low levels of intensity of disturbance are consistent with this model. On the contrary, the spread and growth of *C. racemosa* were drastically reduced in heavily disturbed pools, despite turf-forming algae were still abundant, suggesting that the facilitative effect of algal turfs could have been counteracted by high intensity of disturbance.

According to this model, patterns of abundance of *C. racemosa* should have tracked the abundance of turf-forming algae in pools maintained under low levels of intensity of disturbance, but this was not the case. *C. racemosa* displayed the same ability to invade C pools where the average cover of the turf-forming algae was 20.3% and the LI-LV and LI-HV pools where the turfs covered 45.7 and 58.5% of the substratum, respectively. This result suggests that turf-forming algae do not have to monopolize the substratum to facilitate the establishment of *C. racemosa* in unmanipulated pools, but this positive

effect may be counterbalanced by a slight increase in intensity of disturbance. To disentangle these interactions it will be necessary to examine facilitation along a gradient of abundances of algal turfs in combination with changes in intensity of disturbance. This approach would extend previous experimental studies that have focused mostly on the presence/absence of turfs either in the absence or the presence of disturbance (Ceccherelli et al. 2002; Bulleri and Benedetti-Cecchi 2008). Alternatively, but not mutually exclusively, indirect effects of disturbance mediated by other components of resident assemblages might have contributed to the observed patterns of spread of *C. racemosa*. The larger abundance of encrusting coralline algae in HI treatments, in particular, can be explained with reference to previous evidence indicating that the distribution of these organisms are affected by physical or biological events of disturbance that remove their epiphytes (Paine 1980; Steneck 1986; Kendrick 1991; Dethier 1994). At least two mechanisms may be responsible for inhibitory effects of these algae on *C. racemosa*, potentially contributing to its patterns of invasion in rock pools. First, the increased abundance of encrusting corallines may have reduced the topographic heterogeneity of the substratum, hindering the spread of *C. racemosa*, as further suggested by the greater success of invasion of this alga in three-dimensional algal turfs than in barren habitats reported by Ceccherelli et al. (2002). Second, epithallial sloughing could be responsible for the dislodgment of fragments of *C. racemosa* potentially establishing as epiphytes on encrusting corallines (Keats et al. 1993).

In principle, disturbance may also affect the spread of invasive species indirectly, by influencing species richness in first place. This is the classic biotic resistance hypothesis predicting that diversity enhances the resistance of assemblages to invasions (Elton 1958; Crawley 1987; Levine and D'Antonio 1999) due to a more efficient use of resources by more diverse assemblages and their consequent reduced availability for invaders (Loreau 2000; Fargione and Tilman 2005). In this study, however, the documented difference in the number of native taxa in relation to intensity of disturbance (the difference between HI and LI treatments) was due, on average, to a single taxon (the mean number of native taxa over the period of the study was 9.35 and

8.14, respectively). Such a difference may justify, in terms of relative increment (14.8%), the significant effect of the contrast HI versus LI detected by the analysis, but it could hardly explain the drastic reduction of *C. racemosa* observed in heavily disturbed pools. The resistance of assemblages to invasions can, in fact, be significantly affected by drastic changes in the number of native taxa or in patterns of abundance and distribution of resident functional groups of organisms, as indicated by theoretical (Case 1990) and experimental studies (McGrady-Steed et al. 1997; Tilman 1997; Naeem et al. 2000; Symstad 2000).

Indirect mechanisms mediated by effects of disturbance on other components of native assemblages of rock pools, such as canopy-forming algae, are difficult to hypothesize on the basis of our findings. Reduced invasion by *C. racemosa* could be predictable in conditions of relatively larger cover of canopy-forming species (Andrew and Viejo 1998; Ceccherelli et al. 2000; Valentine and Johnson 2003; Scheibling and Gagnon 2006), but this response variable was not significantly affected by any of the experimental treatments examined in our study. Possible direct and indirect effects of herbivores, such as sea urchins (Trowbridge 1995; Sumi and Scheibling 2005), are also unlikely since they were virtually absent in rock pools during our surveys (M. Incera et al., personal observation).

A main goal of this study was to anticipate possible patterns of spread of *C. racemosa* in rock pools under the climate change scenarios in which the frequency, intensity and temporal variability of extreme meteorological events, such as storms, are predicted to increase (Emanuel 1987; Raper 1993; Michener et al. 1997; Muller and Stone 2001; Benestad 2003). In this respect, our findings lead to the following considerations. First, the negative effect of intensity of disturbance on *C. racemosa* observed in our experiment suggests that climate change should not enhance the colonization of rock pools by this alga. This effect could buffer the influences of concomitant anthropogenic changes, such as the reduction of canopy-forming algae in urban areas and their replacement by algal turfs (Benedetti-Cecchi et al. 2001; Eriksson et al. 2007), potentially facilitating the establishment of *C. racemosa*. It is worth noting, however, that these predictions could be jeopardized by the occurrence of different

concomitant events (Paine et al. 1998). It was documented, for instance, that *C. racemosa* can survive stressing conditions as zygotes or resistant fragments (Ruitton et al. 2005b). Second, the response of *C. racemosa* to climate change in adjacent subtidal habitats will likely play a relevant role in dictating future patterns of invasion of rock pools, since subtidal populations will continue to replenish the rock pool habitat with propagules of the alga. This prediction is consistent with the view that propagule pressure is a key factor influencing the spread of invasive species, both in marine and terrestrial systems (Lockwood et al. 2005; Von Holle and Simberloff 2005; Colautti et al. 2006; Drake and Lodge 2006). Concerning present findings, however, possible differences between experimental treatments due to differences in propagule pressure from subtidal propitious areas have to be excluded on the basis of the presence of *C. racemosa* along the whole subtidal area adjacent to the studied pools (Piazzi and Balata 2009). While emphasizing the effects of mechanical disturbance, our results do not neglect the potential role of other climate-driven abiotic and biotic factors in regulating the invasion dynamics of *C. racemosa*. For instance, rock pools are likely to undergo increasing fluctuations in salinity and temperature if the incidence of extreme rainy events increases in winter and evaporation is exacerbated by higher temperatures in the summer, as predicted under modified climate scenarios. Long-term observations are thus required to ascertain whether the outcomes of the present study correctly predict the fate of populations of *C. racemosa* in the rock pool habitat.

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