

Effects of *Caulerpa racemosa* invasion on soft-bottom assemblages in the Western Mediterranean Sea

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Abstract The present study aimed at evaluating the effects of *Caulerpa racemosa* var. *cylindracea* spread on Mediterranean soft-bottom assemblages. The benthic assemblages colonized by *C. racemosa* were compared with non invaded assemblages at multiple spatial scales. In addition, a manipulative experiment has been conducted over a one-year period in order to compare the structure of native assemblages invaded by the alga with others where the alga has been manually removed and others that were not invaded. Results of both studies showed that Mediterranean soft-bottom assemblages invaded by *C. racemosa* differed from non invaded ones in terms of species composition, abundance and patterns of spatial variability. Moreover, in areas cleaned out from the alga, the benthic assemblages begin to recover their structure and after one year they get more similar to the assemblages observed in non invaded areas. The present paper, taking into account different aspects of *C. racemosa* invasion in Mediterranean soft bottoms, highlighted that the observed increase in alpha diversity did not correspond to an increase in the overall diversity of the studied system. In fact, the loss of beta diversity in invaded sites, together with the spread of species typical of vegetated habitats, may contribute to a homogenization of the Mediterranean coastal system.

Furthermore, a possible role of ecosystem engineer for *C. racemosa* can be hypothesized.

Keywords Biological invasions · *Caulerpa racemosa* · Infauna · Epifauna · Alpha diversity · Beta diversity · Western Mediterranean Sea

Introduction

Biological invasions in marine habitats represent one of the main factors of human-induced global changes (Vitousek et al. 1996, 1997; Occhipinti-Ambrogi and Savini 2003) and a cause of dramatic ecological effects (Carlton 1989, 1999; Abrams 1996; Grosholz 2002). Introduced species can affect both single species via behavioral and morphological changes and the whole community organization. The broad consequences of biological invasions are related to the erosion of biodiversity (Bax et al. 2003). The loss of alpha diversity (as both the number of species and the relative abundance of individuals) and beta diversity (referred to as variability in species composition and abundance among habitats or along gradients, Gray 2000) may lead to a biotic homogenization with deep consequences for the structure and functioning of ecosystems (Airoldi et al. 2008; Olden and Poff 2003). These effects are amplified when invaders are able to modify the structure of habitats, making the effects of their colonization more persistent (Wikstrom and Kautsky 2004;

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Hastings et al. 2007). These species are considered “ecosystem engineers” (Jones et al. 1994; Cuddington and Hastings 2004; Wright and Jones 2006) or “foundations species” (Bruno et al. 2003) because of their ability to modify the abiotic environment and to influence the community organization (Crooks 2002).

Invasive engineering species may affect all kinds of marine habitats (Buschbaum et al. 2006; Wallentinus and Nyberg 2007), but their effects could be mostly serious in bare uncoherent substrate (Crooks 1998; Crooks and Khim 1999). Marine coastal soft-bottoms are particularly affected by invasive habitat-forming plants (Neira et al. 2005). Among seaweeds, *Caulerpa* species, thanks to their stoloniferous structure, may develop on all kind of substrate (Meinesz et al. 1993; Infantes et al. 2010) and they are responsible for worrying invasive events worldwide (Meinesz et al. 2001; Glardon et al. 2008). *Caulerpa taxifolia* (Vahl) C. Agardh colonization on soft bottoms have been widely investigated, and deep modifications in ecosystems related to its role of engineering species have been emphasized (McKinnon et al. 2009; Byers et al. 2010). The colonization of un-vegetated soft bottoms by *C. taxifolia* may lead to deep changes in the structure of infaunal assemblages (McKinnon et al. 2009) and can induce important behavioral responses in native fauna (Wright et al. 2010) as well as complex cascading effects on ecosystem structure and functioning (Gribben et al. 2009).

Caulerpa racemosa var. *cylindracea* (Sonder) Verlaque, Huisman et Boudouresque (Verlaque et al. 2003, *C. racemosa* from here after) represents the most severe invasive event ever known in the Mediterranean Sea in terms of invaded surface and impact on ecosystems (Piazzi et al. 2005a; Klein and Verlaque 2008). The spread of *C. racemosa* and its effects on native benthic assemblages have been widely studied on hard bottoms (Piazzi et al. 2001; Piazzi and Balata 2007, 2009; Klein and Verlaque 2009), while less attention has been focused on soft bottoms, where the knowledge is limited to small-scale correlative investigations or studies focusing on a single taxa (Argyrou et al. 1999; Buia et al. 2001; Sandulli et al. 2004; Vázquez-Luis et al. 2009). However, biological invasions are a complex ecological phenomenon and an exhaustive comprehension of their effects needs both correlative and experimental investigations of a wide range of ecosystem components at different spatial scales (Pauchard and Shea 2006; Mack et al. 2007).

We aimed at evaluating the effects of *C. racemosa* spread on Mediterranean soft-bottom assemblages by means of correlative and experimental approaches. A multifactorial sampling design was used to compare soft-bottom assemblages (both epifauna and infauna) colonized by *C. racemosa* with non invaded assemblages at multiple spatial scales. The following hypotheses were tested: Mediterranean soft-bottom assemblages invaded by *C. racemosa* differed in (i) species composition and abundance, (ii) diversity and (iii) spatial patterns of variability from non invaded assemblages.

Moreover, a manipulative experiment was carried out at a smaller spatial scale over a one-year period in order to compare the structure of native assemblages invaded by the alga with others after algal removal, and others not invaded. We tested the hypothesis that at the end of the study period, the benthic assemblages where the alga has been removed, differed from invaded ones and recovered partially or completely their original structure.

Materials and methods

Descriptive study

Sampling design

The study was carried out in the Tuscan Archipelago National Park (north-western Mediterranean Sea). The archipelago is constituted by seven main islands that have been invaded by *Caulerpa racemosa* at least since year 2005 (authors personal observation). Two of them, Capraia and Elba (approximately 30 km apart), were randomly selected. In each island, two invaded sites and two non invaded sites were randomly chosen at 30 m depth; these sites were hundreds of meters apart and invaded and non invaded sites were interspersed among them. In each site two areas (20 m²) tens of meters distant were randomly chosen.

Sediment characteristics

In each site, three sediment samples were collected for particle size analysis and organic matter content. Sediments were collected by scuba diving, using a Plexiglas corer 30 cm long and 10 cm wide (0.00785 m²) (Gambi et al. 1998; Rossi and

Underwood 2002). Sediment samples were analysed for their particle size according to the Udden-Wentworth Phi classification (Wentworth 1922). Each sample was washed in 16% hydrogen peroxide for 24 h and then wet sieved on a 63 μm mesh to sort out the fine fraction. The sand fraction was sieved through a stack of geological test-sieves ranging from 0 Phi to +4 Phi. The fine fraction being less than 1.6%, was not analysed.

Organic matter content was determined by drying 3 g (40°C for 48 h) of sediment sample. Afterwards these were placed in the furnace and kept at 400°C for 12 h. Once cooled the percentage of dry weight loss was calculated.

Faunal assemblages

Infauna and epifauna sampling was carried out using the same cores (0.00785 m²) previously described for the study of sediment characteristics, paying attention to sample the surface sediment layer (from 0 to 12–15 cm of depth). In each area, 5 replicated plots were randomly sampled in October 2007, at the end of the vegetative period of *Caulerpa racemosa* (Ruitton et al. 2005), for a total of 80 cores. Samples were washed through 0.5 mm mesh sieve and fixed in formalin seawater (6%) before sorting and taxonomic identification of organisms in the laboratory. Whenever possible taxa were identified at species level and the abundance of each taxa was expressed as number of individuals. The abundances of the main classes/phyla were also calculated by summing the abundances of all taxa belonging to each phylum or class.

To evaluate differences between invaded and non invaded assemblages and to see if these differences were consistent at different spatial scales, species composition and abundance were analyzed by Permutational Analysis of Variances (PERMANOVA, Anderson 2001). A 4-way model was used with Condition (invaded vs. non invaded) as fixed factor, Island (2 levels) as random factor crossed to Condition, Site (2 levels) as random factor nested in Condition \times Island, Area (2 levels) as random factor nested in Site. Abundance data was arranged in a species \times plot matrix and a similarity matrix was calculated using the Bray-Curtis index from untransformed data. Pseudo-variance components were calculated for each spatial scale in each condition. The ordination plot of similarity coefficients was obtained

by non-metric multidimensional scaling (nMDS). The SIMPER routine was used to establish which taxa mostly contributed to the dissimilarity between groups (Clarke 1993).

For each plot, alpha diversity was calculated by evaluating the number of species and Margalef index (Margalef 1958). Beta diversity in the two conditions (Invaded and Non Invaded assemblages) was evaluated through both the β_S index and multivariate analyses (Gray 2000). β_S index was calculated as the partitioning of the differences between plots to alpha diversity: $\beta_S = N_C/\lambda$, where N_C = the species richness in the condition C, λ = the average plot species richness in condition C (Gray 2000). Differences in multivariate dispersion between invaded and non-invaded assemblages were tested by PERMDISP analysis considering changes in compositional variability among groups directly interpretable as a change in beta diversity among groups (Anderson 2006; Anderson et al. 2006).

Experimental study

The study was carried out at Elba Island, in the Tuscan Archipelago National Park. On a sandy bottom at 30 m depth, in one of the locations sampled for the descriptive study, two sites (20 m²) hundreds of meters apart were selected. In each site six areas (2.5 m²) were randomly chosen, two for each of the following treatments: assemblages invaded by the alga (Invaded = I), assemblages not invaded (Non Invaded = NI) and invaded assemblages cleared from the alga (Removed = R). The study areas were randomly interspersed among them. The alga was manually eradicated (hand pulled) in October 2007 and R areas were maintained free from the alga throughout the study by periodical (once a month) eradications. After 1 year (October 2008) five replicated plots were randomly sampled in each area following the same methods applied in the descriptive study for a total of 60 cores.

Data on species composition and abundance were analysed by 3-way PERMANOVA with the Treatment (3 levels, I vs. NI vs. R) as fixed factor, Site (2 levels) as random factor crossed to Treatment, Area (2 levels) as random factor nested in the interaction Treatment \times Site. Bray-Curtis dissimilarity index was calculated before analyses. nMDS was used for a graphical representation of results. SIMPER

procedure was used to discriminate which taxa mostly contributed to multivariate patterns. PERMDISP analysis was performed to evaluate changes in beta diversity among treatments.

The total number of organisms per plot and Margalef's index of diversity were analyzed by Univariate Analyses of Variance (ANOVA, Underwood 1997) using the same factors and levels considered in the multivariate analyses. Homogeneity of variance was tested by Cochran's C test.

Results

Descriptive study

Both in invaded and non invaded areas, the seabed sediments were primarily sand followed by gravel, with a percentage of mud never exceeding 1.6%. Gravel percentages between invaded and non invaded areas were markedly different in Elba island with higher values in the areas colonized by *C. racemosa*. Organic matter content varied between 1.20 and 2.0% showing slight differences between invaded and non invaded areas (Table 1).

A total of 3,726 organisms belonging to 169 species were found (see Appendix 1). Annelida (Polychaeta), Arthropoda (Crustacea), Mollusca and Sipunculida were the most abundant taxa, whereas Echinodermata, Cephalocordata and Picnogonida were present with low abundances. In non invaded areas 58 species of Polychaeta, 37 Crustacea and 19 Mollusca were found, while in invaded areas 68, 53 and 28 species were collected, respectively.

Polychaeta, Crustacea and Mollusca were more abundant in invaded areas, whereas the opposite pattern was observed for Cephalocordata (Fig. 1).

PERMANOVA analysis detected significant differences between conditions in terms of species composition and abundance (Table 2). Differences between Islands, Sites and Areas were also significant.

Even if stress values resulted high, the nMDS representation of plots (Fig. 2) based on abundance data showed that the plots collected in non invaded areas were separated from those sampled in invaded areas. In addition the former appeared slightly more scattered than the latter.

SIMPER procedure showed that dissimilarity between conditions was mostly due to a higher abundance in invaded areas of the Polychaeta *Paradoneis armata*, *Glycera alba* and *Sigambra tentaculata*, the Crustacea *Leptocheilia savigny*, *Autonoe spiniventris* and *Phthisica marina* and the Mollusca *Haminoea* sp.; whereas the Polychaeta *Aponuphis bilineata* was more abundant in non invaded assemblages (Table 3).

The percentage pseudo-variance components were higher among plots and lower between islands both for invaded and non invaded assemblages, whilst patterns differed between the two conditions at the intermediate scales investigated (Fig. 3).

The total number of organisms per plot and values of Margalef's index in non invaded assemblages were 32.8 ± 2.4 (mean \pm SE, $n = 40$) and 4.42 ± 0.15 respectively and 60.5 ± 3.3 and 6.64 ± 0.17 in invaded ones.

Value of β_S index resulted 7.5 in non invaded assemblages and 5.6 in invaded assemblages.

Table 1 Organic matter percentages (means \pm SD, $n = 3$) and sediment fraction percentages in invaded and non invaded sites in Elba and Capraia islands

	OM %	Gravel %	Sand %	<63 μm %
<i>Elba Island</i>				
Invaded-site 1	1.45 \pm 0.04	20.06 \pm 1.18	78.34 \pm 0.47	1.59 \pm 0.72
Invaded-site 2	1.20 \pm 0.16	20.46 \pm 1.04	78.63 \pm 1.00	0.91 \pm 0.07
Non invaded-site 1	1.85 \pm 0.20	14.58 \pm 1.53	84.73 \pm 1.88	0.69 \pm 0.78
Non invaded-site 2	1.50 \pm 0.09	15.16 \pm 0.17	83.29 \pm 0.57	1.55 \pm 0.51
<i>Capraia Island</i>				
Invaded-site 1	1.55 \pm 0.05	2.56 \pm 0.25	96.73 \pm 0.38	0.71 \pm 0.35
Invaded-site 2	2.00 \pm 0.01	2.86 \pm 0.16	96.52 \pm 0.63	0.62 \pm 0.48
Non invaded-site 1	1.85 \pm 0.14	3.10 \pm 0.13	96.3 \pm 0.37	0.58 \pm 0.34
Non invaded-site 2	1.50 \pm 0.08	3.20 \pm 0.38	96.29 \pm 0.57	0.51 \pm 0.24

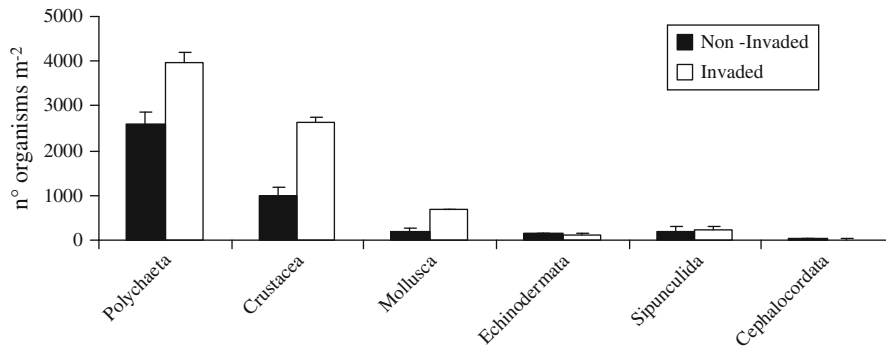


Fig. 1 Descriptive study. Main taxa abundances of macroinvertebrate assemblages in Invaded and Non Invaded areas

Table 2 PERMANOVA examining differences in species composition and abundance between Conditions (Invaded vs. Non Invaded assemblages) at different spatial scales

Source	df	MS	Pseudo-F	P(perm)
Condition = C	1	17,777	3.789	0.002
Island = IS	1	24,978	2.506	0.005
C × IS	1	4,691	0.470	0.988
Site(C × IS) = S(C × IS)	4	9,966	2.282	0.001
Area(S(C × IS))	8	4,366	2.210	0.001
Residual	64	1,975		
Total	79			

Bold = significant results

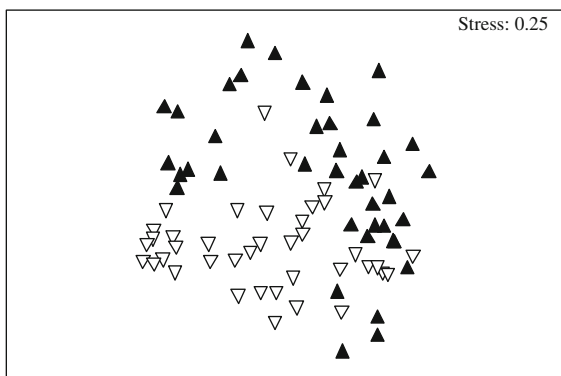


Fig. 2 Descriptive study. Non-metric Multi-Dimensional Scaling ordination plot based on untransformed abundance data. Non Invaded assemblages (black triangles), Invaded assemblages (plain triangles)

Even if the magnitude of the observed differences was low the PERMDISP analysis showed significantly lower average distance from centroids in invaded (52.2 ± 0.6) than in non invaded assemblages (54.7 ± 0.9).

Experimental study

The structure of assemblages was similar to that observed in the descriptive study. A total of 1,950 organisms and 105 species were found. Polychaeta were present with 35, 40 and 45 species in NI, R and I areas respectively, Crustacea with 22, 21 and 36 species, Mollusca with 5, 3 and 7 species. In R areas, Crustacea and Mollusca showed abundances lower than those observed in I areas, whereas on the contrary Polychaeta had higher abundances in areas of algal removal (Fig. 4).

PERMANOVA analyses detected as significant the interaction Treatment × Site (Table 4). Pairwise test showed that both NI and R assemblages were significantly different from I assemblages in both sites; R assemblages were different from NI assemblages in one site only. Although the stress value resulted high, I and NI plots were clearly sorted in the nMDS ordination plot, while R plots were in an intermediate position (Fig. 5).

The SIMPER routine showed that most of the species that contribute to separate I from NI areas (*Leptochelia savigny*, *Apeudes latreilli*, *Exogone verugera*, *Aponuphis bilineata*, *Kefersteinia cirrata*, *Metaphoxus gruneri*, *Glycera alba*, *Branchiostoma lanceolatum*) had comparable abundances in R and NI areas; only the Polychaeta *Caulleriella* sp. and *Paradoneis armata* showed abundances higher in R areas than in the others (Table 5).

PERMDISP showed significant differences among treatments ($F = 6.57$, $P = 0.005$). The average distance from centroids in R assemblages (47.3 ± 1.5) had intermediate values between those found in NI (52.5 ± 1.5) and I assemblages (45.4 ± 1.2).

Table 3 Results of SIMPER routine showing species that mostly contribute to determine differences between invaded and non invaded assemblages (average dissimilarity 81.05%)

Taxa	Mean number of organisms per plot Non invaded	Mean number of organisms per plot Invaded	Contribution (%)
Polychaeta <i>Aponuphis bilineata</i>	5.03	3.65	6.66
Polychaeta <i>Paradoneis armata</i>	3.18	3.88	6.47
Tanaidacea <i>Leptochelia savigny</i>	1.93	3.20	4.30
Polychaeta <i>Sigambra tentaculata</i>	0.53	1.58	2.27
Polychaeta <i>Glycera alba</i>	1.35	1.98	2.22
Gastropoda <i>Haminoea</i> sp	0.15	1.60	2.19
Amphipoda <i>Autonoe spiniventris</i>	0.28	1.53	2.12
Amphipoda <i>Phthisica marina</i>	0.22	1.51	2.10
Polychaeta <i>Eunice vittata</i>	0.03	1.58	1.85
Amphipoda <i>Perioculodes aequimanus</i>	0.13	1.3	1.78
Isopoda <i>Eurydice pulchra</i>	1.33	0.33	1.77
Polychaeta <i>Paraonis fulgens</i>	0.8	0.88	1.76
Decapoda <i>Diogenes pugilator</i>	0.23	1.1	1.69
Polychaeta <i>Kefersteinia cirrata</i>	0.08	1.38	1.68

ANOVA detected as significant the interaction Treatment \times Site for the total number of individuals. SNK test showed that in both sites, differences between I and other treatments were significant, whereas differences between NI and R were significant in one site only; moreover, differences between sites were significant in I and R treatments (Table 6). Significant differences among treatments were detected for the Margalef's index of diversity; SNK test showed that differences between I and the other treatments were significant, while differences between NI and R were not (Table 6).

Discussion

The results of the present study showed that the Mediterranean soft-bottom assemblages invaded by *Caulerpa racemosa* differed from non invaded ones in terms of species composition, abundance and patterns of spatial variability. The patterns detected in the descriptive study were partly corroborated by the findings of the experimental one. After one year from the beginning of the experiment, assemblages in R areas started to recover their structure, becoming more similar to the assemblages found in NI areas than to those found in I ones. This result allows us to infer a cause-effect relationship between the invasion

of *C. racemosa* and the modifications observed in the structure of invaded assemblages.

Invaded assemblages differed from non invaded ones, in terms of number of species and number of organisms mainly belonging to Polychaeta, Crustacea and Mollusca. These results are consistent with those produced by other studies carried out in Mediterranean soft bottoms (Argyrou et al. 1999; Buia et al. 2001; Sandulli et al. 2004; Vázquez-Luis et al. 2009), where in pristine or slightly disturbed locations the presence of *C. racemosa* induced an increase of Crustacea (Vázquez-Luis et al. 2009). Conversely low abundances of Crustacea in sites invaded by *C. racemosa* compared to non invaded ones were detected in areas subjected to other stressors (Argyrou et al. 1999; Sandulli et al. 2004).

An increase in biodiversity and abundance of organisms in areas invaded by *Caulerpa racemosa* seems a general pattern in Mediterranean coastal soft-bottoms. It is well known that biological invasions may cause contrasting effects on native assemblages (Sanchez et al. 2005; Buschbaum et al. 2006). In many cases, the increase of species richness is a consequence of ecosystem modification caused by invading ecosystem engineers. These species may change the environment via their own physical structures (autogenic) or by transforming materials from one state to another by mechanical or other

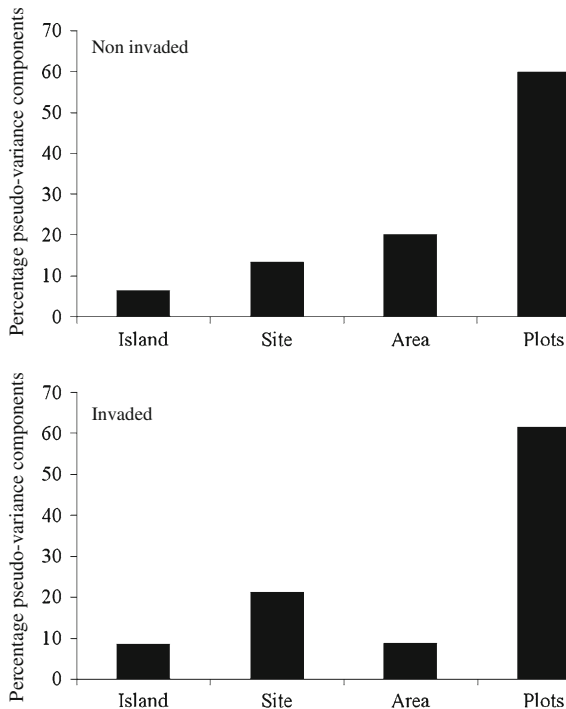


Fig. 3 Percentage pseudo-variance components on species composition and abundance of macroinvertebrate assemblages in the two conditions (Invaded and Non Invaded) at different spatial scales

means (allogenic) (Jones et al. 1994, 1997). *C. racemosa* appears to demonstrate both type of mechanisms (Klein and Verlaque 2008).

Autogenic mechanisms are related to its ability to modify the habitat forming dense mattes of stolons

Table 4 PERMANOVA examining differences in the number of species and abundance between invaded (*I* = Invaded), removed (*R* = Removed) and non invaded (*NI* = Non Invaded) assemblages at different spatial scales (Sites and Areas)

Source	df	MS	Pseudo-F	P(perm)
Treatment = T	2	12,435	1.7597	0.034
Site = S	1	10,803	3.8649	0.001
T × S	2	7,066.3	2.5282	0.001
Area(T × S)	6	2,795	1.3166	0.025
Residual	48	2,122.8		
Total	59			

Pairwise tests			
T × S			
Site1	P(perm)		P(perm)
NI, I	0.002	Non Invaded Site1, Site2	0.085
NI, R	0.992		
I, R	0.001		
		Invaded Site1, Site2	0.001
Site2			
NI, I	0.003		
NI, R	0.002	Removed Site1, Site2	0.002
I, R	0.002		

Bold = significant results

(Klein and Verlaque 2008) and to exert effects dependent on habitat characteristics. For instance, the presence of the stolon mattes formed by *C. racemosa* is able to reduce the habitat complexity of the rocky bottoms and hence their heterogeneity (Piazzi and Balata 2007), whereas the same web can create a converse effect on un-vegetated substrates. In fact the

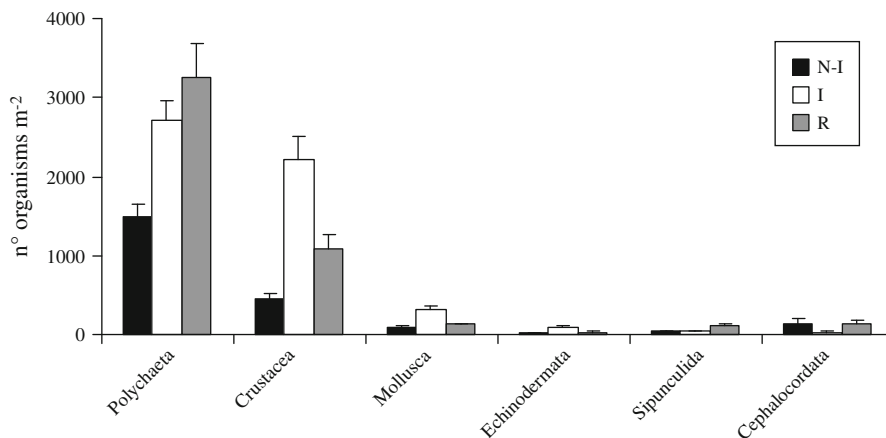


Fig. 4 Experimental study. Main taxa abundances of macroinvertebrate assemblages in the Non Invaded, Invaded and Removed areas after one year from the beginning of the experiment

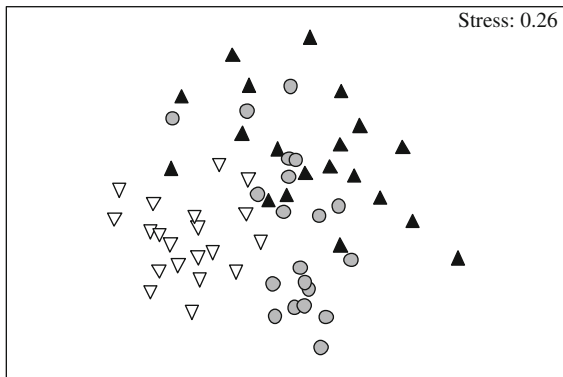


Fig. 5 Experimental study. Non-metric Multi-Dimensional Scaling ordination plot based on untransformed abundance data. Non Invaded assemblages (*black triangles*), Invaded assemblages (*plain triangles*), Removed assemblages (*gray circles*)

presence of algal tangle can build up different microhabitats and shelters, providing new sources of food, promoting the establishment of many zoo-benthic organisms and enhancing the local diversity (Sanchez-Jerez et al. 1999; Bostrom et al. 2006; Mckinnon et al. 2009). The observed increase of small crustaceans (amphipods and tanaids) in our study could be due to the presence of stolons and fronds that act as refuge from predation, whereas the increased food supply may facilitate epifaunal detritivorous such as *Haminoea* sp. and *Diogens pugillator*. These detritivorous species can also be facilitated by the decomposition of algal material that can cause a buildup of nutrients in sediments. This process can be amplified by the activities and mortalities of algal associated organisms (Fukunaga 2008). All these changes in community composition can drive the observed increase of carnivores predators (*Phthisica marina*, *Glycera alba*) in invaded areas that can take advantage from major food availability and predict possible food web changes. Moreover, changes in bottom surface complexity, altering the water movement, can influence the transport of postlarval macrofauna and in turn the structure of assemblages mimicking other invasive engineering species (Commito et al. 2005).

Allogenic mechanisms were mainly observed on rocky bottoms where this alga represents an important trap for sediments, with consequent changes in the substrate characteristics (Piazzi et al. 2005b, 2007). In soft bottoms, this phenomenon has been described for the co-generic *Caulerpa taxifolia*

(Mckinnon et al. 2009) whose changes in sediment quality caused a decrease in infauna abundances. This phenomenon appeared less important for *C. racemosa*, even if the lacking of more exhaustive sediment quality data (i.e. redox potential and PH values) prevent us from corroborating or rejecting these findings. At the same time, we can not exclude that a longer period of colonization could amplify that effect. On the other hand, our results suggest a mechanic effect related to the web created by the stolons and rhizoids of the alga. *Branchiostoma lanceolatum*, for example, seems extremely disadvantaged by the tangle formed by *C. racemosa* because the alga prevents it from sinking fast into the sediment to escape from predators or other source of disturbance. The polychaete *Aponuphis bilineata* seems to respond in a similar way to the algal invasion being negatively affected by the algal rhizoid web that seems to pose a threat to the process of tube building of this annelid worm. An aggregating action on sediment particles of major dimensions exerted by the alga was detectable in the invaded sites on Elba Island where in the immediate surroundings of the rhizoid web the sediment grain size appeared coarser. A possible consequence of this “sediment coarsening” could be an increase in abundance of small or interstitial species (i.e. *Sigambra tentaculata*) that can take advantage from more rapid oxygen turnover and faster metabolic wastes removal.

As a whole our results suggest that the species that can take advantage from the presence of *C. racemosa* are more numerous than those disadvantaged entailing an increase in species richness. Anyway, the observed increase in alpha diversity does not necessarily reflect an ecosystem amelioration, being not, *per se*, a contrasting force to the habitat homogenization (Olden and Poff 2003). In fact, beta diversity resulted lower in invaded assemblages than in non invaded ones. Moreover, although exploring the differences between habitats was not an aim of the present study, our results suggest that the replacement of distinctive assemblages by widespread species or species typical of other habitats like vegetated ones can reduce turnover diversity (between-habitats diversity, Gray 2000) even if alpha diversity may remain the same or increase (Smart et al. 2006). Our results suggest that the observed increase in alpha diversity in invaded assemblages did not correspond to an increase in the overall system diversity.

Table 5 Results of Simper routine showing the species that mostly contribute to determine differences among assemblages in the three treatments (non invaded, invaded, removed). Non

invaded vs invaded av. dissimilarity 79,92%; invaded vs removed av. dissimilarity 76,33%

Taxa		Mean number of organisms per plot Non invaded	Mean number of organisms per plot Invaded	Contribution (%)
Tanaidacea	<i>Leptochelia savigny</i>	0.2	5.55	10.18
Polychaeta	<i>Caulleriella</i> sp.	2.45	1.80	4.68
Isopoda	<i>Apseudes latreilli</i>	1.00	2.15	4.54
Polychaeta	<i>Exogone verugera</i>	0.45	1.90	3.58
Polychaeta	<i>Aponuphis bilineata</i>	1.30	2.15	3.31
Polychaeta	<i>Kefersteinia cirrata</i>	0.20	1.25	2.62
Cephalocordata	<i>Branchiostoma lanceolatum</i>	1.15	0.25	2.59
Amphipoda	<i>Metaphoxus gruneri</i>	0.20	1.25	2.37
Polychaeta	<i>Glycera alba</i>	0.95	1.25	2.29

Taxa		Mean number of organisms per plot Invaded	Mean number of organisms per plot Removed	
Polychaeta	<i>Caulleriella</i> sp.	1.80	8.05	10.09
Tanaidacea	<i>Leptochelia savigny</i>	5.55	0.30	8.25
Polychaeta	<i>Paradoneis armata</i>	0.65	3.15	4.53
Isopoda	<i>Apseudes latreilli</i>	2.15	1.15	3.94
Polychaeta	<i>Exogone verugera</i>	1.90	1.15	3.14
Polychaeta	<i>Aponuphis bilineata</i>	2.15	1.55	2.67
Polychaeta	<i>Kefersteinia cirrata</i>	1.25	1.05	2.36
Polychaeta	<i>Syllis cornuta</i>	0.90	1.15	2.26
Cephalocordata	<i>Branchiostoma lanceolatum</i>	0.25	1.15	2.06
Polychaeta	<i>Glycera alba</i>	1.25	0.40	1.92
Amphipoda	<i>Metaphoxus gruneri</i>	1.25	1.00	1.86

We detected different patterns of spatial variability in the benthic assemblages between invaded and non invaded areas. In non invaded areas, the pseudo-variance components were higher at the smallest scale (i.e. among plots a few decimetres apart) and gradually decreased toward the larger scales. In invaded areas, by contrast, the intermediate scale (i.e. sites hundreds of meters apart) showed a pseudo-variance components higher than expected. This result probably reflects the differences in the intensity of colonization of *Caulerpa racemosa* among sites, a pattern that can be mirrored by the different impacts on the faunal assemblages underneath. In fact even small differences in the algal covering of the substrate can induce different changes in the associated benthic community (Cebrian and Ballesteros 2009).

Furthermore the experimental removal of *Caulerpa racemosa* allowed us to evaluate the recovery abilities of the native benthic assemblages. After 1 year of algal removal, these assemblages do not completely recover their native structure being dominated by several opportunistic taxa, such as *Caulleriella* sp. and *Paradoneis armata*. This pattern is not novel in temperate regions where after an environmental perturbation, the initial colonizers are usually represented by opportunistic Polychaeta (Berge 1990; Ruth et al. 1994). The recovery of soft bottom assemblages seems more effective than that observed on rocky bottoms (Casu et al. 2005; Piazzini and Ceccherelli 2006) even if patterns varied among different taxa. In fact the recovery ability of organisms relies mainly on their life cycles as well as on their ecological adaptation, hence it may vary

Table 6 ANOVA examining differences in the total number of organisms per plot and the Margalef' index of diversity between invaded (*I* = Invaded), removed (*R* = Removed) andnon invaded (*NI* = Non Invaded) assemblages at different spatial scales (Sites and Areas)

Source	<i>df</i>	Number of organisms			Margalef' index		
		MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>
Treatment = T	2	3.97	1.5	0.3999	38.099	26.9	0.0358
Site = S	1	0.0065	0.05	0.8269	0.0003	0	0.9922
Area (S × T)	6	0.1243	1.69	0.1435	2.5826	5.39	0.0003
TxS	2	2.6456	21.28	0.0019	1.4162	0.55	0.6043
Residual	48	0.0735			0.4788		
Total	59						
Cochran's C = 0.190 (NS)					Cochran's C = 0.221 (NS)		
SNK test (T × S)	S1:	NI = R < I	NI:	S1 = S2	SNK test (C)	NI = R < I	
	S2:	NI < R < I	I:	S1 ≠ S2			
			R:	S1 ≠ S2			

Bold = significant results

between different taxa. Species mainly affected by sediment characteristics and/or less mobile taxa such as Polychaeta and Mollusca, may require longer periods to recover compared to highly mobile taxa such as Crustacea. However, the different stages of an invasion, that vary in intensity and extent of colonization, can represent a further source of variability being capable of influencing not only the faunal assemblages underneath but also the re-colonization abilities of benthic organisms (Neira et al. 2007). Therefore, a longer period of *C. racemosa* invasion can lead to more severe impacts with consequent persistent effects on benthic assemblages.

Taking into account different aspects of *Caulerpa racemosa* invasion on Mediterranean soft bottoms, we highlighted other interesting patterns beside those related to changes in community structure. Firstly, a possible role of ecosystem engineer hypothesized for

C. racemosa may represent a relevant ecological aspect since the effectiveness of this invader to drive ecological changes (Bulleri et al. 2010). Secondly, an increase of opportunistic species or species typical of vegetated habitats, together with a reduction of spatial variability and beta diversity could contribute to determine a higher biotic homogenisation in Mediterranean soft bottoms.

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Appendix 1

List of taxa and their relative abundance (mean number of organisms per plot) in Invaded and Non-Invaded areas of the descriptive study

Taxa	Non invaded	Invaded
Platyhelminthes		
<i>Leptoplanas</i> sp.	0.03	0.25
Sipunculida (Aspidosiphonida)		
<i>Aspidosiphon muelleri</i> Diesing, 1851	1.45	1.8
Polychaeta		
<i>Amphiteis gunneri</i> (M. Sars, 1835)	0.1	0.13

continued

Taxa	Non invaded	Invaded
<i>Aonides oxycefala</i> (M. Sars, 1862)	0.08	0.2
<i>Aponuphis bilineata</i> (Baird, 1870)	5.03	3.65
<i>Armandia polyophthalma</i> Kükenthal, 1887	0.1	0.2
<i>Capitella capitata</i> (Fabricius, 1780)	0.23	0.35
<i>Capitomastus minimus</i> (Langherans, 1880)	0.23	0.85
<i>Caulleriella</i> sp.	0.88	0.65
<i>Chaetozone setosa</i> Malmgren, 1867	0.05	0.5
<i>Chone dumeri</i> Malmgren, 1867	0.63	0.68
<i>Chrysopetalum debile</i> (Grube, 1855)	0.03	1.15
<i>Cossura soyeri</i> Laubier, 1962	0.18	0.13
<i>Euclymene oerstedii</i> (Claparède, 1863)	0.23	0.23
<i>Eunice oestedi</i> Stimpson, 1854	0.05	0.35
<i>Eunice vittata</i> (Delle Chiaje, 1828)	0.03	1.58
<i>Exogone verugera</i> (Claparède, 1868)	0.68	0.3
<i>Glycera alba</i> (O. F. Müller, 1776)	1.35	1.98
<i>Kefersteinia cirrata</i> (Keferstein, 1862)	0.08	1.38
<i>Loripes lacteus</i> (Linné, 1758)	0.13	0.28
<i>Lumbrineris latreilli</i> Audouin and Milne-Edwards, 1834	0.48	0.4
<i>Lumbrineris tetraura</i> (Schmarda, 1861)	0.43	0.6
<i>Marphysa belli</i> Audouin and Milne-Edwards, 1833	0.15	0.23
<i>Nematonereis unicornis</i> Schmarda, 1861	0.05	1.3
<i>Orbinia cuvieri</i> (Audouin and Milne-Edwards, 1833)	0.15	0.13
<i>Owenia fusiformis</i> Delle Chiaje, 1841	0.5	0.1
<i>Paradoneis armata</i> Glémarec, 1966	3.18	3.88
<i>Paraonis fulgens</i> (Levinsen, 1883)	0.8	0.88
<i>Phyllodoce lamelligera</i> (Linneus, 1791)	0.23	0.2
<i>Phyllodoce macrophthalma</i> Schmarda, 1861	0.1	0.33
<i>Pisone remota</i> (Southern, 1914)	0.63	0
<i>Platynereis dumerilii</i> (Audouin and Milne-Edwards, 1833)	0.1	1.05
<i>Polycirrus medusa</i> Grube, 1850	0.08	0.15
<i>Prionospio caspersi</i> Laubier, 1962	0.03	0.3
<i>Protodorvillea kefersteini</i> (Mc Intosh, 1879)	0.28	0.45
<i>Sigalion mathildae</i> Audouin and Milne-Edwards, 1832	0.08	0.28
<i>Sigambra tentaculata</i> Treadwell, 1941	0.53	1.58
<i>Sphaerosyllis taylori</i> Perkins, 1981	0.23	0.83
<i>Syllis amica</i> Quatrefages, 1865	0.3	0.73
<i>Syllis cornuta</i> Rathke, 1843	0.45	1.18
<i>Syllis pulvinata</i> (Langerhans, 1881)	0.45	0.25
Mollusca (Gastropoda)		
<i>Ascobulla fragilis</i> (Jeffreys, 1856)	0.23	0.75
<i>Caecum</i> sp.	0.18	0.68
<i>Cypridina mediterranea</i> O.Costa, 1845	0.2	0.58
<i>Haminoea</i> sp.	0.15	1.6
<i>Philine aperta</i> (Linnaeus, 1767)	0.1	0.33
Mollusca (Bivalvia)		

continued

Taxa	Non invaded	Invaded
<i>Lucinella divaricata</i> (Linné, 1758)	0.08	0.33
Crustacea (Tanaidacea)		
<i>Apseudes latreilli</i> (Milne-Edwards, 1828)	0.43	0.18
<i>Leptochelia savigny</i> (Kroyer, 1842)	1.93	3.2
Crustacea (Isopoda)		
<i>Anthura gracilis</i> (Montagu, 1808)	0.05	0.25
<i>Cirolana</i> sp.	0.1	0.15
<i>Eurydice spinigera</i> Hansen, 1890	1.33	0.33
Crustacea (Decapoda)		
<i>Anapagurus breviaculeatus</i> Fenizia, 1937	0.28	0.5
<i>Diogenes pugilator</i> (Roux, 1829)	0.23	1.1
<i>Galathea intermedia</i> Lilljeborg, 1851	0	0.93
<i>Nebalia bipes</i> (O. Fabricius, 1780)	0.03	0.63
<i>Processa</i> sp.	0.18	0.95
Crustacea (Cumacea)		
<i>Cumella limicola</i> Sars, 1879	0.33	0.58
<i>Iphinoe tenella</i> Bate, 1856	0.1	0.33
Crustacea (Copepoda)		
<i>Euterpina acutifrons</i> (Brian, 1921)	0.18	0.23
Crustacea (Amphipoda)		
<i>Autonoe spiniventris</i> (Della Valle, 1893)	0.28	1.53
<i>Cheirocratus sundevallii</i> (Rathke, 1843)	0.08	0.5
<i>Dexamine spinosa</i> (Montagu, 1813)	0.08	0.75
<i>Metaphoxus gruneri</i> Karaman, 1986	0.18	0.53
<i>Orchomene humilis</i> (Costa, 1853)	0.03	0.18
<i>Perioculodes aequimanus</i> (Kossman, 1880)	0.13	1.3
<i>Phtistica marina</i> Slabber, 1769	0.03	0.73
<i>Synchelidium longidigitatum</i> Ruffo, 1947	0.2	0.43
<i>Urothoe elegans</i> Bate, 1857	0.3	0.83
Pycnogonida		
<i>Achelia echinata</i> Hodge, 1864	0.08	0.45
Echinodermata (Ophiuroidea)		
<i>Amphiura chiajei</i> Forbes, 1843	0.08	0.2
Chordata (Cephalocordata)		
<i>Branchiostoma lanceolatum</i> Pallas, 1744	0.38	0.13

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