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The spread of *Caulerpa racemosa* var. *cylindracea* in the Mediterranean Sea: an example of how biological invasions can influence beta diversity

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Abstract

The present study aims to evaluate if invasion of *Caulerpa racemosa* var. *cylindracea* can affect both alpha and beta diversity in Mediterranean coastal system. The following hypotheses were tested: i) measures of alpha diversity differ between invaded and non-invaded assemblages ii) this pattern is consistent between different habitats, iii) assemblages from habitats which are naturally very different tend to be more similar when invaded compared to non-invaded situations. Results showed that Mediterranean benthic assemblages invaded by *C. racemosa* var. *cylindracea* were characterized by lower values of alpha diversity than non-invaded assemblages; moreover, differences between deep (25 m) and shallow water (5 m) assemblages appeared lower in invaded than in non-invaded areas, with a decrease of beta diversity. This homogenisation of habitats was related to a lack of several characteristic species and to a higher abundance of few opportunistic species in invaded areas, particularly turf-forming algae. Moreover, variability in taxa composition was lower in invaded than in non-invaded assemblages in both habitats.

KEY WORDS: beta diversity, biological invasion, *Caulerpa racemosa* var. *cylindracea*, sublittoral, Mediterranean Sea

1. Introduction

Biological invasions represent an important component of human-induced global changes with serious consequences for ecological, economic and social systems (Vitousek et al., 1996; 1997; Occhipinti-Ambrogi and Savini, 2003). In marine systems, biological invasions are particularly severe with usually profound impacts on structure and functioning of ecological systems, by reducing native species richness and altering ecological processes (Ribera and Boudouresque, 1995; Grosholz, 2002; Larned, 2003; Ruesink et al., 2006).

The influences of biological invasions on biodiversity and on the integrity of natural assemblages are widely investigated in aquatic systems (Cohen and Carlton, 1998; Carlton, 1999; Scheibling and Gagnon, 2006). Invaders are normally highly competitive (Rejmánek and Richardson, 1996) and their interaction with native species can cause the extinction or a strong reduction of the latter, leading to a decrease of ecosystem biodiversity (Walker and Kendrick, 1998; Bax et al., 2003). Most of the studies related to biological invasions have used species richness (the number of species in a community) and/or alpha diversity (includes both the number of species and the relative abundance of individuals) as a surrogate of biodiversity (Viejo, 1997; Piazzini and Cinelli, 2003; Casas et al., 2004, Buschbaum et al., 2006). However, biological invasions can influence other aspects of biodiversity. It has been shown that invaded habitats tend to become similar independently of their native characteristics (McKinney, 2004; McKinney and Lockwood, 1999). Consequently, the invasion process causes a decrease of between-habitats diversity (beta diversity) (Gray, 1997). This aspect of biodiversity is considered key to understanding the functioning of ecosystems and to the conservation and sustainable use of biodiversity (Legendre et al., 2005), but it has not been much a focus enough in relation to biological invasions in marine systems.

In the Mediterranean Sea, invasions of the green algae of the genus *Caulerpa* represent an important threat to the biodiversity of benthic coastal systems (Boudouresque and Verlaque

2002). In particular, *Caulerpa racemosa* (Forsskål) C. Agardh var. *cylindracea* (Sonder) Verlaque, Huisman *et* Boudouresque (Verlaque et al., 2003) (*C. racemosa* from here after) has rapidly and successfully invaded wide areas of this basin, forming permanent populations and strongly interfering with native species (Piazzi et al., 2001; 2005b; Ruitton et al., 2005a). *C. racemosa* is able to overgrow other macroalgal species, reaching virtually 100% cover in invaded areas (Piazzi et al., 2001; Balata et al., 2004). This spatial dominance can modify the structure and composition of invaded assemblages and reduce differences between habitats, leading to habitat homogenisation.

The aim of the present study was to evaluate if invasion of *C. racemosa* can affect both alpha and beta diversity. In order to verify these two models, the following hypotheses were tested: i) measures of alpha diversity differ between invaded and non invaded assemblages ii) this pattern is consistent between different habitats, iii) assemblages from habitats which are naturally very different tend to be more similar when invaded compared to non-invaded situations.

2. Material and methods

The study was carried out on the rocky coast of Tuscany, in the north-western Mediterranean Sea. In this geographic area *Caulerpa racemosa* was introduced in 1993 and now the alga colonizes wide zones along the continental and insular coasts from 0 to more than 40 meters in depth (Piazzi et al., 2005b).

We selected two habitats at different depths: 5 m and 25 m. For each of the two habitats, 4 locations about 1000 m² wide and with similar exposure to light, currents and wave energies, were chosen a few km apart. For each habitat, 2 locations were invaded by *C. racemosa* for at least two years, while the other 2 were non-invaded. Invaded and non-invaded locations were interspersed. At each location, two sites of about 100 m² wide and tens of m apart were chosen on horizontal substrata. In each site, three replicated quadrats of 400 cm² were

collected in November 2005 by scraping the substratum with a hammer and a chisel and preserved in formalin. This sampling date was chosen because it is during the peak in biomass production of *C. racemosa*, before the resting winter season (Capiomont et al., 2005; Ruitton et al., 2005b). Algae and sessile invertebrates were identified in the laboratory and their covers determined as percentage of sampling surface covered by vertical projection of each organism.

Alpha diversity was evaluated as the number of taxa per sample and per habitat (point richness and sample richness respectively, *sensu* Gray 2000) and as evenness (expressed as the Pielou's index). Values of point richness and evenness were analysed by 4-way ANOVAs. with Condition (invaded vs. non-invaded) as fixed factor, Habitat (5 m vs. 25 m) as orthogonal and fixed factor, Location (2 levels) as random factor nested in the interaction Condition x Habitat and Site (2 levels) as random factor nested in Location. Homogeneity of variances was checked by Cochran's *C*-test. Student Newman Keuls (SNK) test was used for a posteriori multiple comparison of means (Underwood, 1997).

According to Whittaker (1972), beta diversity can be measured as the variability in species composition among sampling units for a given area at a given spatial scale. Beta diversity was evaluated through a modified version of the Gower's measure of dissimilarity, as described in Anderson et al. (2006). We chose the Gower's measure of dissimilarity because it explicitly weights an order-of-magnitude change in abundance the same as a change in species composition (Anderson et al., 2006). The Gower's measure of dissimilarity was obtained after transforming the data to $x' = \log_2(x) + 1$ for $x > 0$ and $x' = 0$ for $x = 0$, and excluding double zeros. Non parametric multivariate analysis of variance (PERMANOVA) was used to test the hypothesis that assemblages differed between invaded and non-invaded areas and between habitats and to detect eventual interactions between these factors (Anderson, 2001). Factors in the analysis were the same as in univariate analysis.

Differences in multivariate dispersion between invaded and non-invaded assemblages were tested by PERMDISP analysis on the original Gower's matrix being changes in compositional variability among groups directly interpretable as a change in beta-diversity among groups (Anderson, 2006).

A 2-dimensional nMDS (non metric multidimensional scaling) based on the original Gower's matrix was used for a graphical representation of the data (Clarke and Gorley, 2001).

The program IndVal (Indicator Value) was used to determine which species were responsible for the differences between Conditions in each Habitat (Dufrene and Legendre, 1997).

3. Results

A total of 107 taxa were identified, 13 Chlorophyta, 12 Ochrophyta, 72 Rhodophyta, 3 Porifera, 6 Bryozoa, 1 Annelida (Table 1 with, nomenclature authority). The total number of taxa was 62 at 5 m and 82 at 25 m in non-invaded areas and 41 at 5 m and 59 at 25 m in invaded areas. Similarly, the average number of taxa per sample was significantly higher in non invaded than in invaded assemblages and at 25 m compared to 5 m (Fig. 1a). The number of taxa also differed between locations (Table 2). ANOVA detected a significant interaction between Condition and Habitat for evenness (Table 2). SNK test showed that non-invaded assemblages had significantly higher evenness values than invaded assemblages at 5 m but not at 25 m (Fig. 1b).

nMDS showed that, when invaded by *C. racemosa*, assemblages at 5 and 25 m were more similar than when non invaded (Fig. 2), which resulted in a significant interaction between Condition and Habitat (Table 3). The structure of algal assemblages also differed among locations, but samples were more dispersed in non-invaded than in invaded areas in both habitats. PERMDISP showed significantly ($F = 14.15$, $P = 0.001$) lower average distance from centroids in invaded (19.2 ± 0.8) than in non-invaded areas (24.1 ± 0.9).

The IndVal analysis showed that the species that mostly contributed to separate invaded locations from non-invaded ones, were *Womersleyella setacea* at 25 m, *Pterosiphonia pennata* at 5 m and *Cladophora prolifera* and *Halopithis incurva* at both depths (Fig. 3). Other taxa that contributed to differences between non-invaded and invaded assemblages included erect algae (*Halimeda tuna*, *Flabellia petiolata*, *Corallina elongata*), encrusting Bryozoans (*Schizobrachiella sanguinea* and *Schizomavella cornuta*), encrusting algae (*Aglaozonia melanoidea* and Encrusting Corallinaceae) and several turf species, in particular the epilithic Chlorophyta *Pseudochlorodesmis furcellata* (Table 4).

4. Discussion

Both alpha and beta diversity were lower in areas invaded by *Caulerpa racemosa* than in non-invaded areas. The low alpha diversity was related to lower mean number of taxa and evenness per sample. At invaded locations, 19 and 23 taxa were not present at 5 and 25 m respectively, compared to non-invaded locations. Furthermore, assemblages at 5 and 25 m habitats were more similar in invaded than non-invaded areas, and variability in taxa composition was lower in invaded than non-invaded areas at both depths.

A reduction of alpha diversity in assemblages invaded by *C. racemosa* had been already reported (Piazzi et al., 2001; Balata et al., 2004) and differences between invaded and non-invaded assemblages described in this study are similar to those described previously. These effects can be related to the rapid stoloniferous growth of the alga (Ruitton et al., 2005b) that can inhibit the growth of other sessile species. Inhibition can also be enhanced through sediment trapping (Piazzi et al., 2005a; Piazzi et al., 2007).

Conversely, there are no information on the influence of this species on beta diversity. Beta diversity may be caused by random variation in community

composition and/or by gradients of environmental factors (Legendre et al., 2005). The latter case applies to the study system, where shallow Mediterranean assemblages tend to be dominated by photophilous algae, mostly Fucophyceae, with abundant turf and a reduced encrusting layer, while deeper assemblages tend to be dominated by encrusting organisms, mostly red algae belonging to Corallinales and animals with calcareous skeletons (Ballesteros, 2006). The reduction of differences between deep and shallow assemblages in areas invaded by *C. racemosa* was related to the lack of several species unique to the two habitats and to the increased abundance of few opportunistic species. Forty% of the exclusive taxa of the deep habitat and 45% of the taxa exclusive of the shallow habitat were not present in invaded locations, while opportunistic species such as *Cladophora prolifera*, *Halopithys incurva* and several turf-forming species including *Womersleyella setacea* and *Pterosiphonia pennata*, dominated the invaded assemblages at both depths. Many of these opportunistic species are considered tolerant to several kinds of disturbance, such as sediment deposition and burial (Gorostiaga et al., 1998; Airoldi, 1998) which could favour their development in invaded areas. Facilitation of turf-forming species in assemblages invaded by *C. racemosa* has been already described, suggesting a synergism between the invader and turfs (Ceccherelli et al., 2002; Piazzì and Ceccherelli, 2006). We can hypothesize that the development of turf-forming algae

contributed to reduce differences between invaded assemblages, as algal turfs are considered a major components of biotic homogenisation at global scales (Airoldi, 1998; Gorgula and Connell, 2004; Balata et al., 2007).

Although correlative studies such as this cannot identify a cause-effect relationship, the results suggest that Mediterranean habitats invaded by *C. racemosa* tended to lose their natural patterns of variability, leading to a reduction of beta diversity. The loss of spatial variability in different habitats or regions contributes to what is known as “biotic homogenisation” (McKinney and Lockwood, 1999). Biotic homogenisation is considered one of the most prominent forms of biotic impoverishment worldwide and an important aspect in the ecology of invasions (Smart et al., 2006). A loss of alpha and beta diversity, involving the replacement of ecological specialists by widespread generalists, can cause not only a taxonomical homogenization but also a functional homogenisation, with consequent changes in overall community function and a reduction in ecosystem resilience (Olden et al., 2004). Also, homogenisation can be enhanced if the lost species are not randomly distributed among taxonomic and ecological categories (McKinney and Lockwood, 1999).

In the present study, sessile animals were less abundant in invaded than in non-invaded assemblages and Bryozoans were completely absent. Although this relation must be further explored by experimental studies, it represents an important issue related to *C. racemosa* invasion. In fact, the lack of most sessile animals in invaded assemblages can lead to serious functional alterations of invaded ecosystems. Taxonomic and functional homogenisation can reduce the capability of the communities to react to disturbance, increasing the vulnerability to large-scale events, such as environmental alterations or further biological invasions (Cohen and Carlton, 1998). Low functional diversity can also lead to a temporal synchrony in population dynamics and to a

lack of complementary use of resources in time, increasing availability of resources to non-native species (Stachowicz et al., 2002).

Although beta diversity has been less considered than species richness in marine ecological studies, it represents a fundamental aspect of the ecosystems and a good ecological indicator. Biological invasions may cause contrasting effects on assemblages that are difficult to understand, as richness can increase or decrease as a consequence of invasions (Sanchez et al., 2005; Buschbaum et al., 2006). Increased species richness, however, could be a consequence of ecosystem modification caused by invaders, that promote the colonization of opportunistic species or species characteristic of other habitats (Crooks, 2002; Britton-Simmons, 2004). Both increased or decreased species richness could result in a higher homogenisation of habitats. Thus, impact evaluations of biological invasions should consider not only the total number of species present in an area, but also the species identity and their ecological function.

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Fig. 1. Number of species (a) and evenness (b) of non-invaded (white) and invaded (black) assemblages (mean + SE, n = 12).

Fig. 2. Non-metric MDS ordination based on Gower's dissimilarity coefficient applied to species-samples matrix. Circles = assemblages at 5 m depth, Triangles = assemblages at 25 m depth, Grey = non-invaded locations, Black = invaded locations.

Fig. 3. Percentage cover (mean + SE, n = 12) of species that mostly contribute to separate non-invaded assemblages (white) from invaded ones (black).

Table 1. List of taxa. N-I = non-invaded assemblages; I = invaded assemblages. Habitats at water depths of 5 m and 25 m.

Taxa	- 5 m		- 25 m	
	N-I	I	N-I	I
Chlorophyta				
<i>Bryopsis cupressina</i> J.V. Lamouroux	+	-	+	-
<i>Caulerpa racemosa</i> (Forsskål) C. Agardh var. <i>cylindracea</i> (Sonder) Verlaque, Huisman et Boudouresque	-	+	-	+
<i>Chaetomorpha linum</i> (O.F. Müller) Kützing	+	+	-	-
<i>Cladophora echinus</i> (Biasoletto) Kützing	-	-	+	+
<i>Cladophora dalmatica</i> Kützing	+	+	-	-
<i>Cladophora prolifera</i> (Roth) Kützing	+	+	+	+
<i>Codium bursa</i> (Linnaeus) C. Agardh	-	-	+	+
<i>Flabellia petiolata</i> (Turra) Nizamuddin	+	+	+	+
<i>Halimeda tuna</i> (J. Ellis et Solander) J.V. Lamouroux	+	-	+	+
<i>Palmophyllum crassum</i> (Naccari) Rabenhorst	-	-	+	-
<i>Pseudochlorodesmis furcellata</i> (Zanardini) Børgesen	+	-	+	-
<i>Valonia macrophysa</i> Kützing	-	-	+	+
<i>Valonia utricularis</i> (Roth) C. Agardh	+	-	-	-
<u><i>Ochrophyta</i></u>				
<i>Cladostephus spongiosus</i> (Hudson) C. Agardh	+	+	-	-
<i>Cystoseira spinosa</i> Sauvageau	-	-	+	-
<i>Dictyota dichotoma</i> (Hudson) J.V. Lamouroux	+	+	-	-
<i>Dictyota linearis</i> (C. Agardh) Greville	-	-	+	+
<i>Halopteris filicina</i> (Grateloup) Kützing	+	+	+	+
“ <i>Aglaozonia melanoidea</i> (Schousboe ex Bornet) Sauvageau” phase sporophyte of <i>Cutleria adspersa</i> (Mertens ex Roth) De Notaris	+	-	-	-
<i>Nereia filiformis</i> (J. Agardh) Zanardini	-	-	+	+
<i>Padina pavonica</i> (Linnaeus) Thivy	+	-	-	-
<i>Sphacelaria cirrosa</i> (P.H. Roth) C. Agardh	+	+	+	+
<i>Sphacelaria plumula</i> Zanardini	-	-	+	+
<i>Stypocaulon scoparium</i> (Linnaeus) Kützing	+	+	-	-
<i>Zanardinia typus</i> (Nardo) G. Furnari	-	-	+	+
<u><i>Rhodophyta</i></u>				
<i>Acrodiscus vidovichii</i> (Meneghini) Zanardini	-	-	+	+
<i>Acrosorium venulosum</i> (Zanardini) Kylin	+	+	-	-
<i>Acrothamnion preissii</i> (Sonder) Wollaston	+	+	+	+
<i>Aglaothamnion tenuissimum</i> (Bonnemaison) Feldmann-Mazoyer	-	-	+	+
<i>Aglaothamnion tripinnatum</i> (C. Agardh) Feldmann-Mazoyer	+	+	+	-
<i>Amphiroa cryptarthrodia</i> Zanardini	-	-	+	+
<i>Anotrichium barbatum</i> (C. Agardh) Nägeli	+	-	-	-
<i>Antithamnion cruciatum</i> (C. Agardh) Nägeli	+	+	+	+
<i>Antithamnion tenuissimum</i> (Hauck) Schiffner	-	-	+	+
<i>Apoglossum ruscifolium</i> (Turner) J. Agardh	-	-	+	+
<i>Bornetia secundiflora</i> (J. Agardh) Thuret	+	-	-	-
<i>Botryocladia botryoides</i> (Wulfen) Feldmann	-	-	+	+
<i>Centroceras clavulatum</i> (C. Agardh) Montagne	+	+	-	-

<i>Ceramium bertholdii</i> Funk	-	-	-	-
<i>Ceramium circinatum</i> (Kützing) J. Agardh	+	+	+	+
<i>Ceramium diaphanum</i> (Lighfoot) Roth	-	-	+	+
<i>Ceramium flaccidum</i> (Kützing) Ardissonne	+	+	+	+
<i>Ceramium codii</i> (H. Richards) Feldmann-Mazoyer	+	+	+	+
<i>Champia parvula</i> (C. Agardh) Harvey	+	+	+	+
<i>Chondria dasyphylla</i> (Woodward) C. Agardh	+	+	+	+
<i>Chondria capillaris</i> (Hudson) M.J. Wynne	+	-	+	+
<i>Contarinia peyssonneliaeformis</i> Zanardini			+	+
<i>Contarinia squamariae</i> (Meneghini) Denizot	-	-	+	-
<i>Corallina elongata</i> J. Ellis et Solander	+	-	-	-
<i>Corallophila cinnabarina</i> (Grateloup ex Bory de Saint-Vincent) R.E. Norris	-	-	+	-
<i>Crouania attenuata</i> (C. Agardh) J. Agardh	+	+	+	+
<i>Dasya ocellata</i> (Grateloup) Harvey	+	-	+	+
<i>Dasya rigidula</i> (Kützing) Ardissonne	+	+	+	+
Encrusting Corallinaceae	+	+	+	+
<i>Erythroglossum sandrianum</i> (Kützing) Kylin	-	-	+	+
<i>Eupogodon planus</i> (C. Agardh) Kützing	-	-	+	+
" <i>Falkenbergia rufolanosa</i> (Harvey) F. Schmitz " phase sporophyte of <i>Asparagopsis armata</i> Harvey	+	+	+	+
<i>Feldmannophycus rayssiae</i> (Feldmann et Feldmann-Mazoyer) Augier et Boudouresque	+	+	+	+
<i>Gelidium bipectinatum</i> G. Furnari	-	-	+	+
<i>Gelidium spathulatum</i> (Kützing) Bornet	+	-	-	-
<i>Gloiocladia furcata</i> (C. Agardh) J. Agardh	-	-	-	-
<i>Haliptilon virgatum</i> (Zanardini) Garbary et H.W. Johansen	+	+	+	+
<i>Halopithys incurva</i> (Hudson) Batters	+	+	+	+
<i>Halydictyon mirabile</i> Zanardini	-	-	+	+
<i>Herposiphonia secunda</i> (C. Agardh) Ambronn	+	+	+	+
<i>Heterosiphonia crispella</i> (C. Agardh) M.J. Wynne	+	+	+	+
<i>Hypnea musciformis</i> (Wulfen) J.V. Lamouroux	+	+	-	-
<i>Hypoglossum hypoglossoides</i> (Stackhouse) Collins et Harvey	+	+	+	+
<i>Jania adhaerens</i> J. V. Lamouroux	-	-	+	+
<i>Jania rubens</i> (Linnaeus) J.V. Lamouroux	+	+	-	-
<i>Laurencia obtusa</i> (Hudson) J.V. Lamouroux	+	-	-	-
<i>Lomentaria chylocladiella</i> Funk	-	-	+	+
<i>Lomentaria verticillata</i> Funk	+	+	-	-
<i>Meredithia microphylla</i> (J. Agardh) J. Agardh	+	-	+	-
<i>Monosporus pedicellatus</i> (J.E. Smith) Solier	+	+	+	+
<i>Nitophyllum punctatum</i> (Stackhouse) Greville	+	-	-	-
<i>Osmundea pelagosae</i> (Schiffner) F.W. Nam	-	-	+	+
<i>Peyssonnelia rubra</i> (Greville) J. Agardh	+	-	+	+
<i>Peyssonnelia squamaria</i> (S.G. Gmelin) Decaisne	-	-	+	-
<i>Pleonosporium borneri</i> (J.E. Smith) Nägeli	-	-	+	-
<i>Plocamium cartilagineum</i> (Linnaeus) P.S. Dixon	+	+	+	+
<i>Polysiphonia elongata</i> (Hudson) Sprengel	-	-	+	+
<i>Polysiphonia furcellata</i> (C. Agardh) Harvey	+	-	+	+
<i>Polysiphonia perforans</i> Cormaci, G. Furnari, Pizzuto et Serio	-	-	+	-
<i>Polysiphonia subulifera</i> (C. Agardh) Harvey	+	+	-	-
<i>Polysiphonia tripinnata</i> J. Agardh	+	-	-	-

<i>Pterosiphonia pennata</i> (C. Agardh) Sauvageau	+	+	-	-
<i>Ptilothamnion pluma</i> (Dillwyn) Thuret	+	-	+	-
<i>Rhodophyllis divaricata</i> (Stackhouse) Papenfuss	+	-	+	+
<i>Rhodymenia</i> sp.	+	+	-	-
<i>Rodriguezella strafforelloii</i> F. Schmitz	-	-	+	+
<i>Spermothamnion repens</i> (Dillwyn) Rosenvinge	+	-	+	-
<i>Sphaerococcus coronopifolius</i> Stackhouse	+	-	+	-
<i>Spyridia filamentosa</i> (Wulfen) Harvey	+	+	-	-
<i>Symphocladia marchantioides</i> (Harvey) Falkenberg	+	+	-	-
<i>Tricleocarpa fragilis</i> (Linnaeus) Huisman et R.A. Townsend	-	-	+	+
<i>Womersleyella setacea</i> (Hollenberg) R.E. Norris	+	+	+	+
<i>Wrangelia penicillata</i> (C. Agardh) C. Agardh	-	-	+	+
Porifera				
<i>Axinella damicornis</i> (Esper 1794)	-	-	+	-
<i>Cacospongia scalaris</i> (Schmidt 1862)	-	-	+	+
<i>Spirastrella cunctatrix</i> (Schmidt 1868)	-	-	+	-
Bryozoa				
<i>Myriapora truncata</i> (Pallas 1766)	-	-	+	-
<i>Schizobrachiella sanguinea</i> (Norman 1868)	-	-	+	-
<i>Schizomavella cornuta</i> (Heller 1867)	-	-	+	-
<i>Scrupocellaria reptans</i> (Linnaeus 1767)	-	-	+	-
<i>Reteporella beaniana</i> (King 1846)	-	-	+	-
<i>Smittina cervicornis</i> (Pallas 1766)	-	-	+	-
Annelida				
<i>Serpula vermicularis</i> Linnaeus 1757	-	-	+	+

Table 2. Results of 4-way ANOVAs on values of species number and evenness. Significant values are in bold. Condition: non-invaded assemblages (N-I) vs. invaded assemblages (I); Habitat: -5 m vs. -25 m.

Source	df	number of species			evenness		
		MS	F	P	MS	F	P
Condition = C	1	1680.33	34.38	0.023	0.109	24.16	0.001
Habitat = H	1	616.33	12.61	0.004	0.031	83.35	0.008
Location (C x H) = L (C x H)	4	48.87	10.76	0.003	0.001	1.06	0.436
Site (L (C x H))	8	4.54	0.45	0.884	0.001	0.64	0.740
C x H	1	0.75	0.02	0.907	0.143	109.05	0.001
Residual	32	10.18			0.002		
Total	47						
Cochran 's C -test transformation			0.153 none			0.178 none	
SNK test			C: S.E.= 1.427; H: S.E. = 1.427 -5 m > -25 m; N-I > I			C x H: S.E. = 0.010 -5 m: N-I > I -25 m: N-I = I	

Table 3. Results of PERMANOVA on the structure of assemblages. Significant effects are indicated in bold.

Source	df	MS	Pseudo- F_p		Denominator terms
Condition = C	1	55608.00	35.64	0.001	L (C x H)
Habitat = H	1	25456.00	16.32	0.001	L (C x H)
Location (C x H) = L (C x H)	4	1560.30	5.34	0.001	S (L (C x H))
Site (L (C x H)) = S (L (C x H))	8	292.27	0.76	0.871	R
C x H	1	6888.80	4.42	0.005	L (C x H)
Residual = R	32	386.01			
Total	47				

Table 4 . Results of the Indicator Species Analysis (IndVal). Habitats at water depths of 5 m and 25 m.

-5m	
Non-invaded assemblages	Invaded assemblages
<i>Halimeda tuna</i>	<i>Cladophora prolifera</i>
<i>Pseudochlorodesmis furcellata</i>	<i>Pterosiphonia pennata</i>
<i>Aglaozonia melanoidea</i>	<i>Halopithys incurva</i>
<i>Corallina elongata</i>	
Encrusting Corallinaceae	
<i>Dasya rigidula</i>	
<i>Dictyota dichotoma</i>	
<i>Laurencia obtusa</i>	
<i>Herposiphonia secunda</i>	
<i>Symphyclocladia marchantioides</i>	
<i>Acrosorium venulosum</i>	
<i>Ceramium flaccidum</i>	
<i>Valonia utricularis</i>	
<i>Padina pavonica</i>	
<i>Hypnea musciformis</i>	
<i>Feldmannophycus rayssiae</i>	
<i>Gelidium spathulatum</i>	
<i>Peyssonnelia rubra</i>	
-25m	
Non-invaded assemblages	Invaded assemblages
<i>Pseudochlorodesmis furcellata</i>	<i>Cladophora prolifera</i>
Encrusting Bryozoans	<i>Halopithys incurva</i>
<i>Halimeda tuna</i>	<i>Womersleyella setacea</i>
<i>Apoglossum ruscifolium</i>	
<i>Chondria dasyphylla</i>	
<i>Aglaothamnion tenuissimum</i>	
<i>Flabellia petiolata</i>	
<i>Wrangelia penicillata</i>	
<i>Peyssonnelia rubra</i>	
<i>Sphacelaria cirrosa</i>	
<i>Falkenbergia rufolanosa</i>	
<i>Champia parvula</i>	
<i>Lomentaria chylocladiella</i>	
Encrusting Corallinaceae	
<i>Rhodophyllis divaricata</i>	
Erect Bryozoans	
<i>Crouania attenuata</i>	
<i>Contarinia squamariae</i>	
<i>Ceramium codii</i>	
<i>Chondria dasyphylla</i>	
<i>Ptilothamnion pluma</i>	

Figure 1

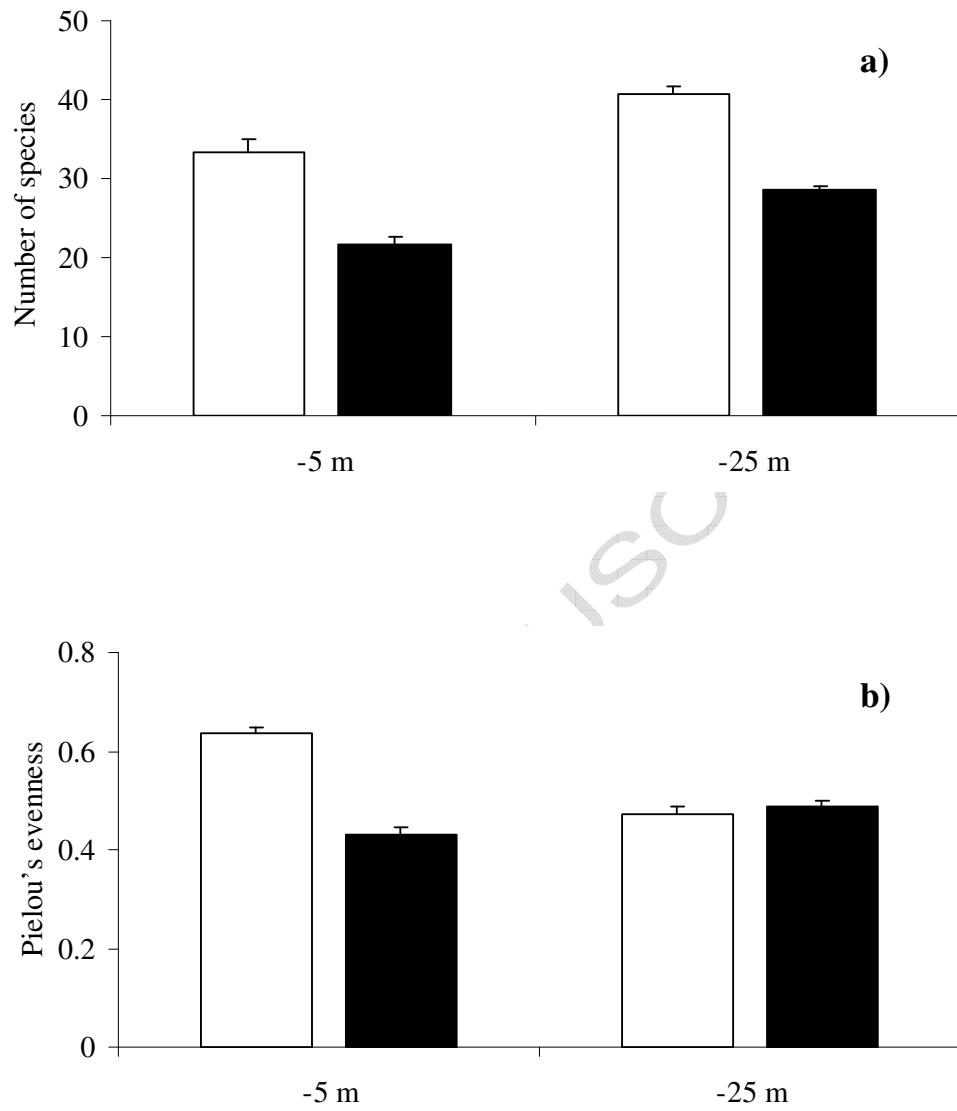


Figure 2

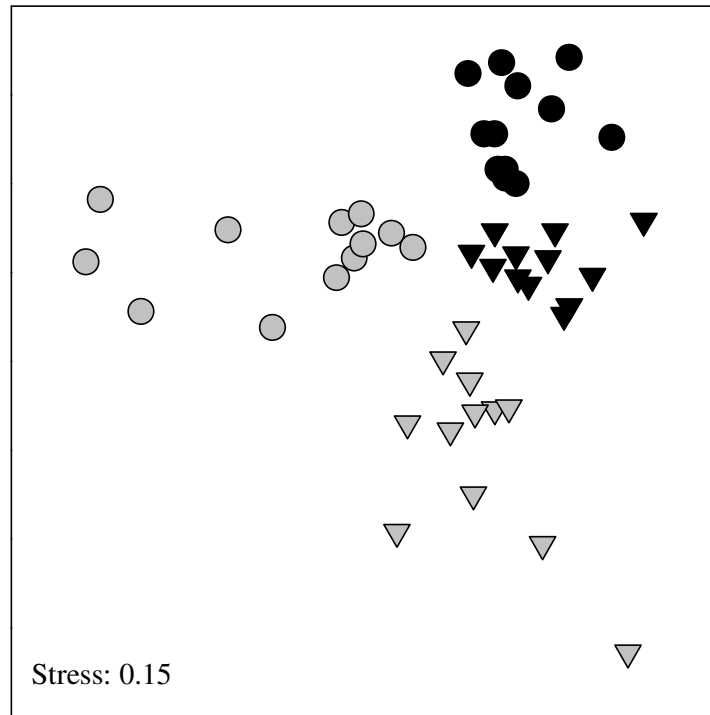


Figure 3

