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Loss of fucoid algae along a gradient of urbanisation, and structure of benthic assemblages

L. Mangialajo*, M. Chiantore, R. Cattaneo-Vietti

Dipartimento per lo Studio del Territorio e delle sue Risorse, Università degli Studi di Genova, C.^{so} Europa 26, 16132 Genova, Italy

ABSTRACT: Canopy-forming macroalgae of the genus *Cystoseira* are being lost in several areas of the Mediterranean Sea. *Cystoseira amentacea* var. *stricta* and *C. compressa* are common species in the Ligurian Sea; they are distributed in patches, but their abundance and distribution is locally variable. We investigated changes in relative cover, biomass and morphology of *Cystoseira amentacea* var. *stricta* and *C. compressa* with increasing urbanisation, and effects of the presence or absence of *Cystoseira* species on the composition and structure of understorey assemblages. *C. amentacea* var. *stricta* habitats were lost close to urban areas, while *C. compressa* slightly increased. The morphological characteristics of these 2 species were very variable in space and time, and did not vary with urbanisation. Assemblages lacking canopy differed markedly from *Cystoseira*-dominated assemblages, particularly assemblages dominated by *Corallina elongata,* the species most responsive to changes in habitat structure and urbanisation, which forms dense turfs in urban habitats lacking canopies. Marked species-specific differences between the assemblages dominated by the 2 *Cystoseira* species were detected. *C. amentacea* var. *stricta* is a key species maintaining habitat complexity and species diversity in Mediterranean rocky shores and we recommend additional conservation actions, such as habitat restoration by transplantation of this endangered species.

KEY WORDS: *Cystoseira amentacea* var. *stricta* · *Cystoseira compressa* · *Corallina elongata* · Fucoid algae · Habitat loss · Structuring role · Urbanisation

INTRODUCTION

Canopy-forming brown algae, in particular Fucales and Laminariales, are habitat formers on understorey assemblages, modifying physical and biological factors (Reed & Foster 1984, Ballesteros et al. 1998, Jenkins et al. 1999a,b, Bulleri et al. 2002) and leading to biological habitat amelioration (*sensu* Moore et al. 2007), but their loss is reported worldwide (Steneck et al. 2002, Airoldi & Beck 2007).

The genus *Cystoseira* (Fucales) is represented by 45 species (Guiry & Guiry 2007), most of them endemic to the Mediterranean Sea (Barceló et al. 2000). They represent the highest level of Mediterranean seaweed complexity, are long-lived (Clayton 1990, Ballesteros et al. 2002), can reach high biomass values (Ballesteros 1989), and dominate in several communities (Giaccone & Bruni 1973); therefore they are generally considered the 'Mediterranean kelps.'

Loss of low shore *Cystoseira* assemblages in the Mediterranean Sea has been shown in a large number of studies (for a short review see Thibaut et al. 2005). Species of *Cystoseira* seem to be sensitive to a variety of environmental stressors, as a consequence of which, they are now used in ecological status assessment (*sensu* Water Framework Directive 2000/60/EU, Ballesteros et al. 2007, Mangialajo et al. 2007). The ecological consequences of the loss of *Cystoseira* species on understorey assemblages, however, are little known.

In the Ligurian Sea (NW Mediterranean), *Cystoseira amentacea* var. *stricta*, (hereafter *C. amentacea*) and *C. compressa* form non-continuous belts at low shore level. They are patchily distributed, with the upper limit of *C. compressa* distribution generally occurring

*Email: luisama@dipteris.unige.it

above that of *C. amentacea* var. *stricta*, but their relative abundance and distribution are locally variable, due to erratic recruitment and interactions of abiotic and biotic factors at different spatial scales (Benedetti-Cecchi et al. 1996, 2000). *C. amentacea*, endemic to the Mediterranean Sea, is very sensitive to changes in water quality (Pinedo et al. 2007, and references therein), while *C. compressa* shows a wider distribution (present also in the Atlantic Ocean) and seems to be more tolerant. It has been suggested that one of the first noticeable effects of urban wastewater pollution is the replacement of *C. amentacea* var. *stricta* by *C. compressa* (Giaccone 1993); along the Albères coast, Thibaut et al. (2005) recorded the loss of all *Cystoseira* spp. (including *C. mediterranea*, vicariant of *C. amentacea*), except for *C. compressa.* The replacement of *C. amentacea* by *C. compressa* has also been observed following large-scale experimental removals of *Cystoseira* canopies (mostly *C. amentacea*) by Benedetti-Cecchi et al. (2001).

Coastal development in Europe is among the major drivers of the loss of complex macroalgal beds, mainly due to the degradation of water quality (Airoldi & Beck 2007). The Ligurian Sea coastline has been historically very urbanised, which has led to severe modifications of natural rocky coastline, as well as pollution, local eutrophication, and increased water turbidity. Urbanisation increases towards Genova city; which is reflected by gradients in water column characteristics (in particular an increase of nutrients and faecal bacteria, Mangialajo et al. 2007), but knowledge of the effects of urbanisation on canopy-forming macroalgae and associated species is limited. The aim of this study was to test whether the relative cover, biomass and morphology of *Cystoseira amentacea* and *C. compressa* changed along a gradient of urbanisation of the coastline, and whether the composition and structure of understorey assemblages differed in relation to the presence or absence of *C. amentacea* and *C. compressa*, taking into account any such differences along the same gradient of urbanisation.

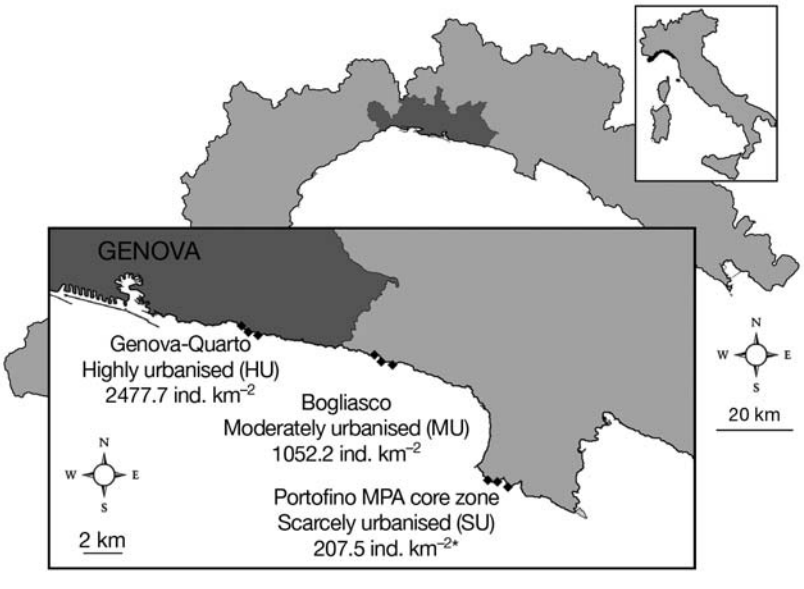

Fig. 1. Location of the 3 shores along the urban gradient near Genova city, together with inhabitant densities; *density at Portofino village, 5 km east of the core zone

MATERIALS AND METHODS

Sampling. The study was performed in a microtidal environment (tidal amplitude around 30 cm) in the typical Mediterranean infralittoral fringe (Pérès & Picard 1964). Three sections of shoreline about 1.5 to 2 km long, characterised by the presence of both *Cystoseira amentacea* and *C. compressa*, were selected along an increasing gradient of inhabitant density and distance from the city of Genova (Fig. 1), as in Mangialajo et al. (2007): Genova Quarto (highly urbanised, HU), Bogliasco (moderately urbanised, MU) and Portofino (scarcely urbanised, SU). All sections have natural carbonatic rocky bottoms (limestone in HU and MU, pudding stone in SU) and similar geographical exposition, fetch and exposure to wave action. Within each section, we chose at random 3 sites about 300 to 500 m long and hundreds of meters apart, and for each site we considered 3 types of habitats: (1) *C. amentacea,* (2) *C. compressa,* (3) absence of fucoid algae. Percentage cover of *C. amentacea* and *C. compressa* was estimated along 10 independent 20 m transects at each site in May 2004 by quantifying the proportion of coastline covered by dense clumps of either *C. amentacea* or *C. compressa*, or lacking fucoids.

Biomass and morphological features of *Cystoseira amentacea* and *C. compressa* were quantified in patches where populations showed high densities (canopy cover between 80 and 100%). In order to limit disturbance to these endangered species, primary axes were cut near the holdfast in 3 replicate 400 cm^2 plots for each site. The surface covered by holdfasts was visually quantified *in situ*, while lengths of 10 randomly chosen axes and primary branches were measured in the laboratory. Biomass was calculated as dry weight (after 48 h at 70°C). To avoid overweight due to epiphytes (mostly articulated Corallinales), branches and axes were roughly cleaned with a pair of tweezers, slightly centrifuged and treated with hydrochloric acid (4%) for 60 min.

The composition of understorey assemblages in each habitat was analysed by sampling three 400 cm^2 plots at each site. Percentage cover of understorey species was visually estimated by using a frame with twenty-five 4 × 4 cm subquadrats (Meese & Tomich 1992, Dethier et al. 1993) after the removal of canopies of *Cystoseira*. Mobile animals (except limpets) were not considered. When the identification to the species level was not possible *in situ*, specimens were collected and identified in the laboratory; in order to reduce the sampling effort, some organisms were grouped in taxonomic or morphological groups, hereafter called taxa.

Due to the high seasonal variability of biomass of fucoids and associated algal diversity, the studies of biomass, morphological features, and structure of assemblages were conducted twice, in spring (May 2004), when biomass and algal diversity are highest, and in autumn (October 2004), at the beginning of the *Cystoseira* resting period.

Data analysis. The full models (including the factor Time) in both univariate and multivariate analyses would have not provided the correct denominators to test the effects of Habitat and Urbanisation, and of their interaction. In order to avoid complicated pooling procedures, we chose to analyse the 2 sampling times separately, because temporal variability is not specifically addressed in our hypotheses.

For the univariate analyses on biomass and holdfast cover, for each sampling time the ANOVA model included 2 factors: Urbanisation (fixed, orthogonal) and Site (random, nested in Urbanisation). Analyses on axis and branch lengths included the additional factor, Plot (random, nested in Site).

Changes in the composition of understorey assemblages were tested by multivariate analyses. For each sampling time, the model included 3 factors: Habitat (fixed, orthogonal), Urbanisation (fixed, orthogonal) and Site (random, nested in Urbanisation). Differences among assemblages were tested by non-parametric ANOVA (PERMANOVA, Anderson 2001) on a Bray-Curtis similarity matrix calculated on square-root transformed data. PERMANOVA p values were obtained from Monte Carlo asymptotic-permutation distributions (Anderson & Millar 2004). The relative importance of each factor in the analysis was assessed using estimates of the magnitude of effect sizes of fixed factors, based on mean squares of the full model (Underwood 1997, Anderson & Millar 2004), expressed as the ratio among the effect size of each fixed factor (θ^2_i) and the sum of the effect sizes of all fixed factors and their interactions. In our case, the factor magnitude was expressed by the formula $\theta^2_i/\Sigma(\theta^2_{Ha} + \theta^2_{Ur} + \theta^2_{Ha \times Ur})$, where i corresponds, alternatively, to Habitat (Ha), Urbanisation (Ur) or their interaction (Ha × Ur).

Multivariate patterns of distribution were plotted using a principal coordinates analysis (PCO, Anderson 2003) on Site centroids, while SIMPER analysis was performed to identify the species most responsible for the differences between the 3 habitats. Species diversity was estimated as $\log_2$ based Shannon-Wiener diversity index (*H'*, Shannon & Weaver 1949) and ANOVA was applied to test for significant effects of Habitat and Urbanisation. All the multivariate analyses were performed using PRIMER software (Clarke & Gorley 2006).

RESULTS

Percentage cover of habitats dominated by *Cystoseira amentacea* or *C. compressa* and habitats lacking fucoids at the 3 shores along the urbanisation gradient are reported in Fig. 2. Percentage of cover by *C. amentacea* decreased along the urbanisation gradient from nearly 50% at SU to less than 10% at HU, while percentage of cover by *C. compressa* showed the opposite trend, increasing from less than 10% cover at SU to about 20% at HU. Percentage of habitats lacking fucoids was high all along the urbanisation gradient, exceeding 70% of rocky bottoms at HU.

While overall canopy cover changed notably along the urbanisation gradient, the biomass or morphological characteristics of the 2 species of *Cystoseira* within each habitat did not seem to vary as much (Fig. 3, Table 1). The only exception was axis length of *C. compressa*, which significantly increased from SU to HU in both May and October. Also in October, length of branches of *C. compressa* increased slightly but significantly from SU to HU; this pattern was not observed in May (Table 1, SNK tests). Overall, biomass and branch length showed high variability at the lowest spatial

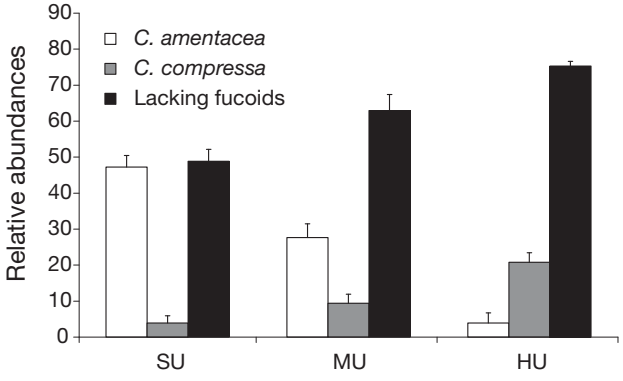

Fig. 2. *Cystoseira amentacea* and *C. compressa*. Relative abundance and habitats lacking fucoids along the urbanisation gradient: scarcely urbanised, SU; moderately urbanised, MU; highly urbanised, HU (error bars: SE)

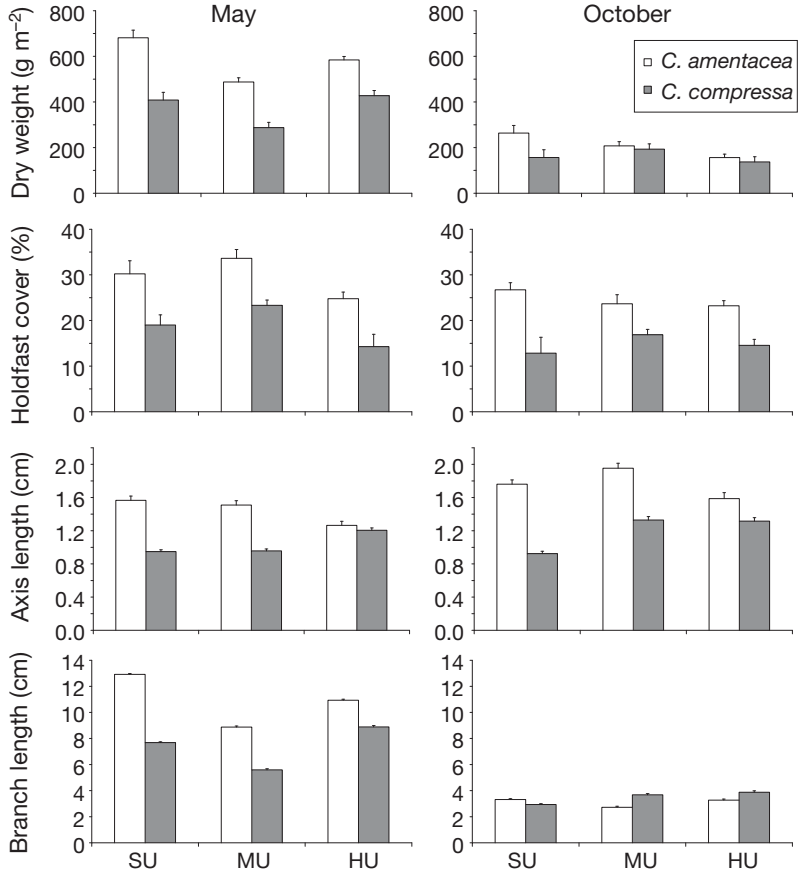

Fig. 3. *Cystoseira amentacea* and *C. compressa*. Biomass and morphological features along the urbanisation gradient. Abbreviations as in Fig. 2 (error bars: SE)

scales (Site and Plot, respectively) and between the 2 sampling times. In May, *C. amentacea* showed longer branches and axes, and higher holdfast cover (and consequently, higher biomass) than *C. compressa*, while in October there were smaller differences between the 2 species, especially for branch length and biomass.

Overall, 83 taxa were visually sampled in the 3 assemblages; they were grouped in 52 variables for the data analysis (Table 2). PERMANOVA (Table 3) showed significant differences in the structure of understorey assemblages as a function of both Habitat and Urbanisation. In May, an interaction between these 2 terms was recorded, showing that the structure of the understorey assemblage always differed significantly between habitats dominated by any *Cystoseira* spp. and habitats lacking canopies, while differences between the 2 canopies of *Cystoseira* were significant only at MU (Table 4). The structure of understorey assemblages in habitats dominated by either of the 2 *Cystoseira* species was always significantly different among the 3 levels of urbanisation, while in habitats lacking canopies, it was more homogeneous (Table 4). In October a strong urbanisation effect was recorded, while the effects of habitat varied among sites; nevertheless, at all sites, the strongest differences were always found between habitats dominated by *C. amentacea* and habitats lacking fucoids (Table 5). *C. compressa* habitat seemed to represent an intermediate state, being in some cases not significantly different from the *C. amentacea* habitat and in other cases not significantly different from habitat lacking fucoids. The relative magnitude of the 2 main fixed factors (Habitat and Urbanisation) at both sampling times highlighted the larger effect of Habitat (0.52 in May and 0.66 in October) in affecting variability in the understorey assemblages. Urbanisation effect was lower at both sampling times (0.31 in May and 0.28 in October) and the interaction between the 2 factors had the lowest weight (0.18 in May and 0.06 in October).

The relevance of the 2 factors is portrayed by PCO of site centroids (Fig. 4). The species that mostly drove the distribution of points along this axis was *Corallina elongata* (together with *Hypnea musciformis* in October), which was associated with habitats devoid of fucoids in HU. In contrast, invertebrates, encrusting corallinales and other light-sensitive algae (e.g. *Valonia utricolaris* and *Pterocladiella capillacea*) were associated to *Cystoseira amentacea* habitats, especially in SU. The second axis was mostly driven by photophilic algae, including species belonging to the genus *Dictyota* and to the *Laurencia* complex, which were associated with habitats lacking fucoids in SU. The SIMPER analysis (Table 6) highlighted that *Corallina elongata* was the species mostly contributing to discrimination among the different habitats and urbanisation levels. Also, thin, articulated and encrusting corallinales, *Hypnea musciformis*, mussels, barnacles and vermetids contributed to among group dissimilarity.

The abundances of *Corallina elongata* and of invertebrates are reported in Fig. 5 and the corresponding ANOVA in Table 7. At both sampling times, *Corallina elongata* increased from SU to HU, while invertebrates showed the opposite pattern, particularly in May. *Corallina elongata* was by far the most abundant species in habitats lacking fucoids (reaching >90% of cover at HU in May) and its abundance significantly decreased in habitats of *Cystoseira compressa* and even more in habitats of *Cystoseira amentacea*, where it reached values

Table 1. *Cystoseira amentacea* and *C. compressa*. Biomass and morphological features. **Bold**: significant.; $^{*}p < 0.05$, $^{**}p < 0.01$, ns = not significant

Source	df	*Cystoseira amentacea*						*Cystoseira compressa*						Denominator
		May			October			May			October			MS
		MS	*F*	p	MS	*F*	p	MS	*F*	p	MS	*F*	p	
Dry weight														
Urbanisation	2	132.2332	1.02	0.4162	6.0360	2.19	0.1927	10977.4444	2.97	0.1267	2.4253	0.11	0.8960	Plot(Ur)
Site(Ur)	6	129.8825	5.44	**0.0023**	2.7513	5.74	**0.0017**	3692.1852	2.86	**0.0389**	21.6760	3.97	**0.0105**	Res
Res	18	23.8712			0.4790			1290.3704				5.4533		
Tot	26													
		Transf.: none; Cochran's test: ns			Transf.: none; Cochran's test: ns			Transf.: none; Cochran's test: ns			Transf.: none; Cochran's test: ns			
Holdfasts cover														
Urbanisation	2	178.7315	6.42	**0.0324**[a]	32.6759	0.52	0.6207	184.6204	1.90	0.2294	37.2870	0.84	0.4760	Plot(Ur)
Site(Ur)	6	27.8611	0.54	0.7720	63.2130	1.32	0.2967	97.1481	3.10	**0.0290**	44.2685	2.28	0.0819	Res
Res	18	51.7130			47.7130			31.3426			19.4167			
Tot	26													
		Transf.: none; Cochran's test: ns			Transf.: none; Cochran's test: ns			Transf.: none; Cochran's test: ns			Transf.: none; Cochran's test: ns			
Axis length														
Urbanisation	2	2.3164	1.70	0.2604	1.3202	4.16	0.0735	1.9183	6.60	**0.0305**[b]	1.0567	30.87	**0.0007**[c]	Site(Ur)
Site(Ur)	6	1.3642	1.39	0.2734	0.3171	0.69	0.6571	0.2906	1.61	0.2011	0.0342	0.41	0.8596	Plot(Si × Ur)
Plot(Si × Ur)	18	0.9846	6.41	**0.0000**	0.4565	5.03	**0.0000**	0.1803	4.55	**0.0000**	0.0825	4.01	**0.0000**	Res
Res	243	0.1535			0.0907			0.0396			0.0206			
Tot	269													
		Transf.: ln(x); Cochran's test: ns			Transf.: none; Cochran's test: < 0.01			Transf.: sq.rt.; Cochran's test: ns			Transf.: none; Cochran's test: < 0.05			
Branches length														
Urbanisation	2	367.2693	2.41	0.1702	10.6807	4.19	0.0727	8.4964	8.97	**0.0135**[d]	1.5665	5.22	**0.0485**[e]	Site(Ur)
Site(Ur)	6	152.1492	3.87	**0.0118**	2.5500	2.46	0.0644	0.8863	1.50	0.2336	0.2999	1.67	0.1854	Plot(Si × Ur)
Plot(Si × Ur)	18	39.3376	10.38	**0.0000**	1.0347	2.46	**0.0011**	0.5527	20.58	**0.0000**	0.1794	6.30	**0.0000**	Res
Res	243	3.7903			0.4207			0.0264			0.0285			
Tot	269													
		Transf.: none; Cochran's test: ns			Transf.: none; Cochran's test: < 0.01			Transf.: sq rt.; Cochran's test: < 0.05			Transf.: sq rt.; Cochran's test: ns			

SNK tests: [a]MU > HU (*); SU, MU and SU, HU: ns; [b]HU > MU, SU (*); [c]SU < HU, MU (**); [d]MU < HU, SU; [e]SU< HU, MU

near 5% at SU (Fig. 5). Invertebrates were inversely affected by habitat, being most abundant in habitats of *Cystoseira amentacea* and significantly decreasing in habitats of *Cystoseira compressa* and even more in habitats lacking fucoids. In May, invertebrates decreased linearly from SU to HU, while in October, although always significantly less abundant at HU, invertebrates were more abundant at MU than SU (Fig. 5). This pattern was mostly driven by mussels (SU: 3.5% ± 1.3; MU: 6.9% ± 2.1; HU: 2.8% ± 0.9).

Overall diversity of understorey assemblages decreased significantly as a function of both Urbanisation (maximal diversity at SU, minimal at HU) and Habitat (maximal diversity in habitats of *C. amentacea*, minimal in habitats lacking canopies, Fig. 6). In May (period of maximum algal development in the Mediterranean Sea), there was an interaction between the 2 factors (Table 8), which can be explained by lack of differences between the 2 *Cystoseira* habitats at SU.

DISCUSSION

Several factors have been suggested to trigger the loss of large brown algae, including urbanisation and eutrophication (Munda 1993, Benedetti-Cecchi et al. 2001, Soltan et al. 2001), increase in water turbidity and sedimentation (Vogt & Schramm 1991, Eriksson et al. 2002, Airoldi 2003, Schiel et al. 2006), overgrazing (Jenkins et al. 1999a,b, Benedetti-Cecchi et al. 2000, Steneck et al. 2002, Thibaut et al. 2005, Hereu 2006) and climate change (Serio et al. 2006, Moore et al. 2007). While this study is correlative and therefore cannot reveal cause–effect relationships, urbanisation remains the most plausible explanation for the observed patterns, highlighting that some *Cystoseira* spp. are more sensitive than others to coastal urbanisation. Our results indicate that *C.*

Table 2. Taxa found with visual census and their grouping for data treatment. Taxa reported in parentheses were identified in the laboratory

Taxon	Species	Acronym
Ocrophyta	*Colpomenia sinuosa*	Col
	Filamentous phaeophyta (*Sphacelaria tribuloides*)	FP
	Dictyota spp. (*D. dichotoma*, *D. fasciola*)	Dic
	Dictyopteris polypodioides	D.po
	Stypocaulon scoparium	Sty
	Taonia atomaria	Tao
	Padina pavonica	Pad
Chlorophyta	*Bryopsis duplex*	Bry
	Caulerpa racemosa	Cau
	Cladophora spp. (*C. albida*, *C. coelothrix*, *C. hutchinsiae*, *C. laetevirens*)	Cla
	Filamentous chlorophyta (*Flabellia petiolata*[a], *Pseudochlorodesmis furcellata*)	FC
	Ulva spp. (*U. compressa, U. laetevirens*)	Ulv
	Valonia utricularis	Val
Rhodophyta	*Apoglossum ruscifolium*	Apo
	Chondracanthus acicularis	C.ac
	Chondria spp. (*C. boryana*, *C. capillaris*, *C. dasyphylla*)	Cho
	Corallina elongata	Cor
	Encrusting corallinales (*Lithophyllum incrustans*, *Neogoniolithon brassica-florida*)	EC
	Filamentous rhodophyta (*Boergeseniella fruticulosa*, *Callithamnion granulatum*, *C. tetragonum*, *C. rubrum*, *Dasya* cfr *corymbifera*, *Falkenbergia rufolanosa*, *Ceramium ciliatum*, *Feldmannophycus rayssiae, Lophosiphonia cristata*, *L. obscura*, *Polysiphonia* spp., *Pterosiphonia parasitica*)	FR
	Gastroclonium clavatum	Gas
	Grateloupia filicina	Gra
	Hypnea musciformis	Hyp
	Laurencia complex - cylindrical (*L. intricata*, *L. obtusa*, *Chondrophycus thuyoides*)	LCC
	Laurencia complex - flat (*Osmundea truncata*, *O. verlaquei*)	LCF
	Lithophyllum byssoides	Lit
	Peyssonnelia spp.	Pey
	Porphyra spp. (*P. leucosticta*, *P. umbelicalis*)	Por
	Pterocladiella capillacea	Pte
	Rhodymenia ardissonei	Rho
	Schottera nicaeensis	Scho
	Schyzimenia dubi	Schy
	Scinaia furcellata	Sci
	Small *Gelidium* like (*Gelidiella pannosa*, *Gelidium crinale*, *G. pusillum*)	Gel
	Thin articulated corallinales (*Amphiroa rigida*, *Haliptilon virgatum*, *Jania corniculata*, *J. rubens*)	TAC
	Wrangelia penicillata	Wra
Mixed algal OTU	Encrusting non corallinales (*Aglaozonia stadium*, *Hildenbrandia* spp., *Ralfsia* spp.)	ENC
Anellida	Gregarian serpulids (*Filograna* sp.)	GS
	Individual serpulids	IS
Arthropoda	Barnacles (*Balanus perforatus*)	Bar
Bryozoa	Encrusting bryozoans (*Schizobrachiella sanguinea*)	EB
Cnidaria	Actiniarians	Act
	Aglaophenids-plumularids (*Aglaophenia kirchenpaueri*)	Agl
	Corynactis viridis	C.vir
	Hydrozoans (other)	Hyd
	Paracoryne huvey	Par
Mollusca	*Gastrochaena dubia*	G.du
	Mussels (*Mytilus galloprovincialis*, *Mytilaster* spp.)	Mus
	Limpets (*Patella* spp., *Fissurella* spp.)	Lim
	Vermetids (*Vermetus triquetrus*)	Ver
Porifera	*Cliona* spp.	Cli
	Encrusting sponges	ES
Tunicata	Didemnids (*Didemnum maculosum*)	Did

[a]This species was included in the group Filamentous chlorophyta because only its filamentous form was found in the samples

Table 3. PERMANOVA on understorey benthic assemblages. **Bold**: significant p values. *Cystoseira amentacea* habitat = CA; *C. compressa* habitat = CC; habitat lacking fucoids = NC

Source of variation	df	May			October			Denominator MS
		MS	*F*	p	MS	*F*	p	
Habitat	2	25241.426	26.4851	**0.0001**	22545.9773	22.0482	**0.0001**	Ha × Si(Ur)
Urbanisation	2	16166.822	9.2084	**0.0001**	10839.5802	5.8641	**0.0009**[c]	Si(Ur)
Site(Ur)	6	1755.669	2.5099	**0.0016**	1848.463	3.4403	**0.0001**	Res
Ha × Ur	4	3749.058	3.9338	**0.0016**[a]	1684.061	1.6469	0.1044	Ha × Si(Ur)
Ha × Si(Ur)	12	953.042	1.3625	0.0888	1022.5758	1.9032	**0.0028**[b]	Res
Residual	54	699.499			537.2916			
Total	80							

A posteriori comparisons: [a]Habitat × Urbanisation: see Table 4; [b]Habitat × Site(Ur): see Table 5; [c]Urbanisation: SU, MU: p = 0.2148; SU, HU: p = 0.0139; MU, HU: p = 0.0130

Table 4. *A posteriori* comparisons (p values) for the significant Habitat × Urbanisation interaction (May, Table 3)

	Factor Habitat patch				Factor Urbanisation		
	SU	MU	HU		CA	CC	NC
CA, CC	0.1187	0.0055	0.0873	SU, MU	0.0185	0.0136	0.0583
CA, NC	0.0049	0.0019	0.0092	SU, HU	0.0155	0.0034	0.0090
CC, NC	0.0185	0.0281	0.0141	MU, HU	0.0205	0.0291	0.4404

Table 5. *A posteriori* comparisons (p values) for Habitat × Site(Ur) significant interaction (October, Table 3); test for Habitat effect within each level of factor Site(Ur). Levels: Site A, B and C within each level of factor Urbanisation (SU, MU and HU)

	SU A	SU B	SU C	MU A	MU B	MU C	HU A	HU B	HU C
CA, CC	0.0386	0.0506	0.3150	0.0221	0.0148	0.0121	0.1941	0.0176	0.2859
CA, NC	0.0151	0.0208	0.0024	0.0041	0.0027	0.0016	0.0131	0.0012	0.0402
CC, NC	0.0976	0.0309	0.0198	0.3452	0.0503	0.0206	0.0153	0.0091	0.1882

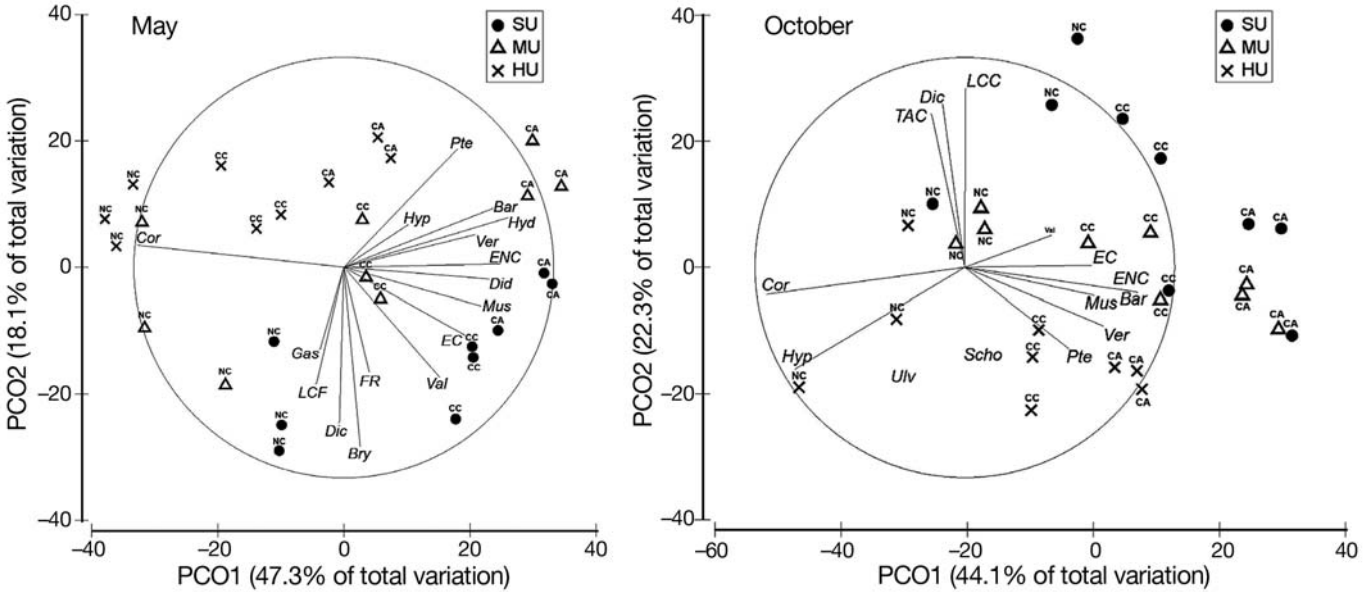

Fig. 4. PCO of site centroids. Abbreviations for urbanisation levels as in Fig. 2. *Cystoseira amentacea* habitats = CA; *C. compressa* habitats = CC; habitats lacking fucoids = NC. Other abbreviations: see Table 2

amentacea habitats were lost close to urban areas, in agreement with previous observations (Thibaut et al. 2005, Arèvalo et al. 2007 and references therein), while *C. compressa* slightly increased, as also observed by Giaccone (1993) and Thibaut et al. (2005). The slightly increased abundance of *C. compressa* close to urban areas could be due to reduced competition with *C. amentacea*.

While habitat cover changed notably along the urbanisation gradient, the biomass and morphological characteristics of the 2 species of *Cystoseira* did not vary as much, and we observed a high variability at small spatial scales and between times, as is common in *Cystoseira* spp. (Ballesteros 1988, Pizzuto et al. 1995). Only the length of axes of *C. compressa* increased towards the most urbanised shore. This could be related to possible release from competition with *C. amentacea*, but we cannot exclude effects of other environmental factors. Manipulative experiments involving cross-transplantation of the 2 species will be necessary to clarify the causes of these patterns.

Overall, the results of the present study suggest that while loss of *Cystoseira amentacea* is a good indicator of anthropogenic effects related to coastal urbanisation, *C. compressa* probably is not, due to its more complex responses. Biomass and morphological features of the 2 species cannot be considered good indicators due to their high variability in space and time.

Benthic understorey assemblages were significantly affected by changes in the distribution of *Cystoseira* species along the urbanisation gradient. Lack of any of the 2 species of *Cystoseira* was the factor mostly affecting assemblage structure, but there were also marked differences between the 2 *Cystoseira* habitats. The species

Table 6. SIMPER analysis on understorey benthic organisms contributing to average dissimilarity between habitats. Ab: average abundance; Dis: average dissimilarity; Dis/SD: consistency to the average dissimilarity in all pairwise comparisons of samples (values >1 indicate a high degree of consistency). Cum %: cumulative percentage contribution to dissimilarity. *Cystoseira amentacea* habitat = CA; *C. compressa* habitat = CC; habitat lacking fucoids = NC. Species abbreviations: see Table 2

C. amentacea vs. *C. compressa*						*C. amentacea* vs. Lacking fucoids					*C. compressa* vs. Lacking fucoids				
Species	CA Ab	CC Ab	Dis	Dis/SD	Cum%	Species	CA Ab	NC Ab	Dis	Dis/SD	Cum%	Species	CC Ab	NC Ab	Dis	Dis/SD	Cum%
Cor	13.02	35.42	13.01	1.48	22.77	Cor	13.02	60.57	25.03	2.09	33.91	Cor	35.42	60.57	14.63	1.53	28.32
TAC	5.41	4.72	3.53	1.07	28.94	TAC	5.41	10.84	5.97	0.9	42	TAC	4.72	10.84	5.73	0.87	39.4
EC	9.11	11.4	3.45	1.12	34.97	Bar	7.85	0.79	3.81	1.24	47.16	EC	11.4	3.49	4.42	1.32	47.95
Mus	7.4	3.49	3.43	1.09	40.98	EC	9.11	3.49	3.49	1.5	51.88	Hyp	4.31	6.47	3.51	0.94	54.76
Bar	7.85	2.75	3.38	1.12	46.88	Hyp	3.25	6.47	3.43	0.86	56.53	ENC	5.06	1.03	2.26	1.11	59.12
Pte	6	0.78	3.21	0.89	52.5	Mus	7.4	1.58	3.42	1.19	61.17	Dic	1.67	3.89	2.08	0.58	63.15
Did	4.78	2.94	3.04	0.79	57.83	ENC	6.99	1.03	3.23	1.36	65.54	Mus	3.49	1.58	1.86	0.78	66.75
ENC	6.99	5.06	2.52	1.16	62.23	Pte	6	0	3.15	0.91	69.81	FR	2.21	2.42	1.7	0.67	70.04
Hyp	3.25	4.31	2.48	1	66.56	Did	4.78	0	2.51	0.63	73.2	LCF	2.36	2.44	1.68	0.85	73.29
Hyd	3.8	1.3	2.25	0.81	70.5	Ver	4.43	0.35	2.25	0.92	76.25	LCC	2.51	2.22	1.55	0.7	76.3
Ver	4.43	2.73	1.91	0.9	73.84	Dic	0.47	3.89	2.05	0.52	79.03	Did	2.94	0	1.49	0.54	79.18
LCF	1.2	2.36	1.53	0.68	76.51	Hyd	3.8	0.11	1.98	0.72	81.72	Gas	1.64	2	1.4	0.63	81.89
Val	2.86	1.03	1.45	0.47	79.04	LCF	1.2	2.44	1.5	0.67	83.74	Ver	2.73	0.35	1.32	0.96	84.44
FR	1.38	2.21	1.4	0.8	81.49	FR	1.38	2.42	1.49	0.58	85.76	Bar	2.75	0.79	1.29	1.04	86.94
LCC	0.5	2.51	1.31	0.6	83.78	Val	2.86	0.29	1.41	0.45	87.68	Bry	1.56	1.7	1.18	0.57	89.23
Gas	0.4	1.64	0.96	0.69	85.46	LCC	0.5	2.22	1.17	0.56	89.27	Cho	0.94	1.52	1.03	0.44	91.22
Dic	0.47	1.67	0.96	0.61	87.13	Gas	0.4	2	1.08	0.47	90.73	Hyd	1.3	0.11	0.68	0.51	92.54
Bry	0.66	1.56	0.94	0.63	88.77	Bry	0.66	1.7	1.04	0.49	92.14	Val	1.03	0.29	0.53	0.42	93.57
C.ac	1.21	0.43	0.71	0.52	90.02	Cho	0.23	1.52	0.85	0.34	93.29	Pte	0.78	0	0.4	0.48	94.35
Cho	0.23	0.94	0.57	0.53	91.01	C.ac	1.21	0	0.64	0.47	94.16	Ulv	0.69	0.09	0.36	0.29	95.04
EB	0.73	0.33	0.52	0.44	91.92	Scho	0.86	0	0.45	0.44	94.77						
Scho	0.86	0.09	0.51	0.47	92.82	Agl	0.81	0	0.42	0.35	95.34						
Agl	0.81	0.17	0.5	0.38	93.69												
Ulv	0.39	0.69	0.47	0.35	94.51												
Gel	0.67	0.31	0.45	0.44	95.3												
Average dissimilarity = 57.16						Average dissimilarity = 73.81						Average dissimilarity = 51.67					

Table 6 (continued)

Species	SU Ab	Groups SU & MU MU Ab	Dis	Dis/SD	Cum%	Species	SU Ab	Groups SU & HU HU Ab	Dis	Dis/SD	Cum%	Species	MU Ab	Groups MU & HU HU Ab	Dis	Dis/SD	Cum%
Cor	20.09	35.97	10.08	1.05	18.42	Cor	20.09	52.94	17.43	1.79	28.53	Cor	35.97	52.94	11.94	1.51	25.78
TAC	9.57	7.09	5.53	0.94	28.53	TAC	9.57	4.31	5.2	0.85	37.04	TAC	7.09	4.31	3.99	1.05	34.39
EC	10.04	7.36	3.27	1.08	34.51	Hyp	1.78	7.08	3.64	0.92	42.99	Hyp	5.17	7.08	3.8	1.07	42.59
Did	4.89	1.51	2.8	0.67	39.62	EC	10.04	6.6	3.14	1.1	48.12	EC	7.36	6.6	2.55	1.1	48.09
Mus	5.35	4.55	2.73	0.88	44.61	Did	4.89	1.32	2.81	0.64	52.71	Ver	4.27	0.69	2.17	0.82	52.77
Hyp	1.78	5.17	2.62	1.02	49.4	Mus	5.35	2.57	2.47	0.77	56.76	Bar	5	1.99	2.14	0.74	57.39
Val	4.1	0.03	2.22	0.63	53.46	ENC	5.71	2.62	2.34	0.98	60.6	Mus	4.55	2.57	2.05	0.95	61.82
Dic	4.42	1.1	2.2	0.63	57.49	Dic	4.42	0.51	2.24	0.6	64.25	ENC	4.75	2.62	1.93	0.96	65.98
Bar	4.4	5	2.14	0.86	61.39	Val	4.1	0.05	2.23	0.62	67.9	Pte	3.03	2.29	1.64	0.63	69.53
ENC	5.71	4.75	2.09	1.01	65.21	LCF	3.29	2.06	2.04	0.85	71.24	Hyd	2.59	0.69	1.5	0.56	72.76
LCC	3.51	1.7	1.93	0.84	68.73	Bar	4.4	1.99	1.96	0.89	74.43	Did	1.51	1.32	1.28	0.53	75.53
FR	2.98	2.06	1.89	0.73	72.18	LCC	3.51	0.02	1.79	0.74	77.37	FR	2.06	0.97	1.24	0.8	78.2
Ver	2.55	4.27	1.84	0.83	75.54	FR	2.98	0.97	1.63	0.64	80.03	LCF	0.66	2.06	1.23	0.63	80.86
Pte	1.46	3.03	1.82	0.55	78.86	Bry	3.05	0.24	1.57	0.68	82.6	Cho	1.77	0.01	0.89	0.37	82.77
Hyd	1.93	2.59	1.78	0.68	82.11	Pte	1.46	2.29	1.38	0.55	84.86	LCC	1.7	0.02	0.87	0.51	84.65
LCF	3.29	0.66	1.68	0.76	85.19	Ver	2.55	0.69	1.32	0.99	87.01	C.ac	0.19	1.44	0.82	0.55	86.42
Bry	3.05	0.64	1.61	0.71	88.13	Gas	2.23	0.7	1.26	0.55	89.07	Gas	1.1	0.7	0.77	0.69	88.08
Gas	2.23	1.1	1.31	0.6	90.52	Hyd	1.93	0.69	1.15	0.6	90.95	Dic	1.1	0.51	0.73	0.57	89.66
Cho	0.92	1.77	1.14	0.5	92.61	C.ac	0.01	1.44	0.81	0.52	92.27	Ulv	0	1.18	0.64	0.45	91.05
Agl	0.48	0.5	0.47	0.38	93.47	Ulv	0	1.18	0.63	0.45	93.31	Cla	0.12	0.96	0.54	0.44	92.2
EB	0.18	0.66	0.42	0.36	94.24	Cla	0.04	0.96	0.51	0.42	94.14	EB	0.66	0.24	0.44	0.38	93.16
Wra	0.56	0.08	0.31	0.53	94.8	Cho	0.92	0.01	0.47	0.53	94.92	Bry	0.64	0.24	0.43	0.49	94.08
Gel	0.3	0.41	0.3	0.65	95.35	Gel	0.3	0.33	0.32	0.32	95.43	Scho	0.38	0.44	0.38	0.38	94.9
												Gel	0.41	0.33	0.37	0.37	95.7
		Average dissimilarity = 54.71						Average dissimilarity = 61.11						Average dissimilarity = 46.32			

that most responded to changes in habitat structure and urbanisation was *Corallina elongata*, a common species in the northwestern Mediterranean Sea (see also Benedetti-Cecchi & Cinelli 1992, Benedetti-Cecchi et al. 2001). This species reached very high cover (>90%) in habitats lacking fucoids at the highly urbanised shore, while at the scarcely urbanised shore it was less abundant (<50% cover), and became nearly absent in *Cystoseira amentacea* habitats (<5% cover), where it was replaced by invertebrates and light-sensitive algae. The greater diversity of understorey species under fucoid canopies, especially in *C. amentacea* habitats, suggests that these species may have a particularly important role in the amelioration of biological habitat (*sensu* Moore et al. 2007), preventing dominance by *C. elongata* and offering shelter to a variety of species. Conversely, canopies of *Cystoseira compressa* did not seem to exert such a strong effect on understorey species and were less effective in preventing colonisation by *C. elongata*. Algal turfs, including those originated by *C. elongata* have been suggested to inhibit the recruitment of many canopy-forming algae (Kennelly 1987, Airoldi 1998, Connell 2005). Although the concept of alternate stability is controversial (Scheffer et al. 2001 and references therein), turfs of corallinales and canopy algae have been proposed as alternative states in temperate reefs (Airoldi 2003, Connell 2005); this study supports the hypothesis that coastal urbanisation could be a driver of shifts between canopy habitats and turfs.

Science and management demand simplified representation of complex systems, but such simplification depends on correct understanding of natural history (Dayton & Sala 2001, Dayton 2003). The results of the present study strongly indicate that it is important to differentiate among different species of *Cystoseira* in ecological studies, not only because of their different responses to anthropogenic impacts, but also because they seem to have different 'engineering' effects on understorey assemblages. Therefore, species

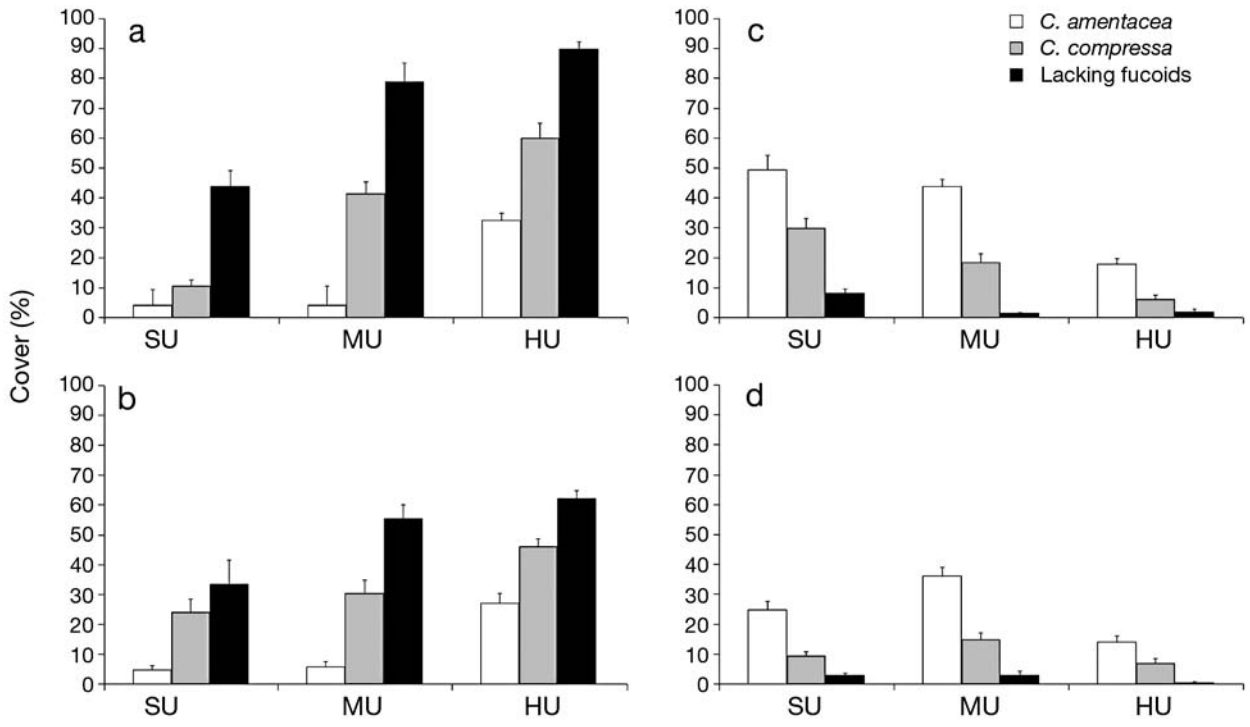

Fig. 5. Percentage cover of *Corallina elongata* (a: May, b: October) and invertebrates (c: May, d: October). Abbreviations as in Fig. 2 (error bar: SE)

Table 7. ANOVA of percentage cover in *Corallina elongata* and invertebrates. **Bold**: significant; *p < 0.05, **p < 0.01, ns = not significant

Source of var.	df	May			October			Denominator MS
		MS	*F*	p	MS	*F*	p	
Corallina elongata								
Habitat	2	22342.57	135.92	0.0000	9708.88	52.24	**0.0000**[b]	Ha × Si(Ur)
Urbanisation	2	11547.56	38.36	0.0004	4057.19	12.39	**0.0074**[c]	Si(Ur)
Site(Ur)	6	301.03	2.29	0.0484	327.51	2.34	0.0439	Res
Ha × Ur	4	845.52	5.14	**0.0120**[a]	282.79	1.52	0.2575	Ha × Si(Ur)
Ha × Si(Ur)	12	164.38	1.25	0.2750	185.84	1.33	0.2294	Res
Residuals	54	131.48			139.73			
Tot	80							
		Transf.: none; Cochran's test: ns			Transf.: none; Cochran's test: ns			
Invertebrates								
Habitat	2	7526.94	71.24	0.0000	3653.6759	148.50	0.0000	Ha × Si(Ur)
Urbanisation	2	2874.44	48.83	0.0002	798.1759	15.63	0.0042	Si(Ur)
Site(Ur)	6	58.87	1.31	0.2692	51.0617	1.66	0.1500	Res
Ha × Si	4	528.89	5.01	**0.0132**[d]	237.1852	9.64	**0.0010**[e]	Ha × Si(Ur)
Ha × Si(Ur)	12	105.65	2.35	**0.0165**	24.6034	0.80	0.6510	Res
Residuals	54	44.98			30.8457			
Tot	80							
		Transf.: none; Cochran's test: ns			Transf.: none; Cochran's test: ns			

A posteriori comparisons: [a]Habitat × Urbanisation: Habitat: SU: NC > CC, CA (**); MU, HU: NC > CC > CA (**); Urbanisation: CA: HU > MU, SU (**); CC: HU > MU > SU (**); NC: HU, MU > SU (**); [b]Habitat: CA < CC < NC (**); [c]Urbanisation: SU < HU (**); MU < HU (*); SU, MU: ns; [d]Habitat × Urbanisation: Habitat: SU, MU: NC < CC < CA (**); HU: NC, CC < CA (*); Urbanisation: CA: HU < MU, SU (**); CC: HU < SU (**), HU < MU (*), MU < SU (*); NC: ns; [e]Habitat × Urbanisation: Habitat: SU, HU: NC < CC (*), NC < CA (**), CC < CA (**); MU: NC < CC < CA (**); Urbanisation: CA: HU < SU < MU (**); CC: HU, SU < MU (**); NC: ns

Table 8. ANOVA on Shannon-Wiener diversity index (*H'*). *Cystoseira amentacea* habitats = CA; *C. compressa* habitats = CC; habitats lacking fucoids = NC. **Bold**: significant; *p < 0.05, **p < 0.01, ns = not significant

Source of variation	df	May			October			Denominator MS
		MS	*F*	p	MS	*F*	p	
Habitat	2	11.0337	89.1749	**0.0000**	4.6460	60.8895	**0.0000**[b]	Ha × Si(Ur)
Urbanisation	2	4.9749	20.2485	**0.0021**	1.1582	13.0984	**0.0065**[c]	Si(Ur)
Site(Ur)	6	0.2457	2.8361	0.0179	0.0884	2.2656	0.0506	Res
Ha × Ur	4	0.7050	5.6976	**0.0083**[a]	0.1111	1.4565	0.2755	Ha × Si(Ur)
Ha × Si(Ur)	12	0.1237	1.4283	0.1820	0.0763	1.9550	0.0476	Res
Residuals	54	0.0866		0.0390				
Total	80							
		Transf.: none; Cochran's test: ns			Transf.: none; Cochran's test: ns			

A posteriori comparisons: [a]Habitat × Urbanisation: Habitat: SU: NC < CC, CA (**); MU, HU: NC < CC < CA (**); Urbanisation: CA: HU < MU, SU (*); CC: HU < MU (*), HU, MU < SU (**); NC: HU, MU < SU (**); [b]Habitat: CA > CC > NC (**); [c]Urbanisation: SU, MU > HU (**)

identity has to be taken into account in implementing monitoring actions (i.e. 'ecological status' assessment, *sensu* Water Framework Directive of the European Union). *C. amentacea* var. *stricta* is a key species in maintaining habitat complexity and species diversity in Mediterranean Sea low shores. This species is protected by the Bern Convention (Council of Europe 1979), but current protection measures do not seem sufficient to stop its current retreat (Thibaut et al. 2005) and we recommend that further conservation actions (i.e. restoration of lost substrata by transplantation, Susini et al. 2007) be seriously considered.

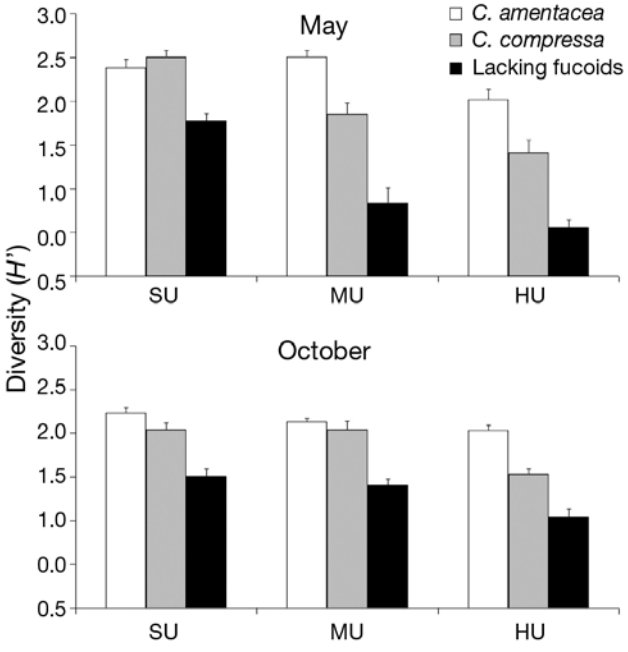

Fig. 6. Shannon-Wiener diversity index (*H'*) along the urban gradient in the 3 habitats. Abbreviations as in Fig. 2 (error bars: SE)

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