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Sediment deposition dampens positive effects of substratum complexity on the diversity of macroalgal assemblages



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ABSTRACT

A three-year experimental study was performed to evaluate the interactive effects of topographic complexity and sedimentation in determining the structure of rocky macroalgal assemblages. The following hypotheses were tested: i) the structure of macroalgal assemblages varies according to the complexity of the substratum; ii) high sediment deposition reduces variations in the structure of assemblages among substrata characterized by different complexity. At natural levels of sediment deposition, greater substratum complexity enhanced species richness and favored the development of assemblages dominated by architecturally complex species, such as large corticated Rhodophyta. Under high sediment deposition, turfs became the main component of macroalgal assemblages, although different filamentous forms responded differently to substratum complexity. In addition, high sediment deposition increased the abundance of the invasive Chlorophyta, *Caulerpa cylindracea*, on low complexity substrata, but decreased it on high complexity substrata. These results show that an increase in sediment deposition can dampen variations between assemblages associated to substrata characterized by different complexity, with consequent reduction of both alpha (i.e., species loss) and beta diversity (i.e., decreased small-scale variation in community structure).

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1. Introduction

Patterns of species distribution and abundance are determined by the interaction between physical and biotic factors (Benedetti-Cecchi et al., 2000; Bertness and Callaway, 1994; Menge and Sutherland, 1987). The role played by natural factors, either physical or biotic, can be, however, deeply altered by anthropogenic perturbations (Chapman et al., 1995; Fujimaki et al., 2009). Thus, understanding the mechanisms structuring communities and how these are modified by anthropogenic pressures represents a main goal for the conservation and management of biodiversity (Gray, 2000; Kumar and Ram, 2005; Martone and Wasson, 2008).

In marine rocky habitats, topographic heterogeneity and complexity (Beck, 2000) are widely acknowledged to be important determinants of species distribution and abundance and, ultimately, of community diversity (Archambault and Bourget, 1996; Beck, 1998; Lapointe and Bourget, 1999; Witman and Dayton, 2001). Substratum complexity can, in fact, modulate biotic interactions, such as competition (Walters and Wethey, 1986), predation (Gosselin and Bourget, 1989) and grazing (Benedetti-Cecchi and Cinelli, 1995), and influence patterns of settlement and/or recruitment of macroalgae and epibenthic invertebrates (Bourget and Harvey, 1998; Bourget et al., 1994; Lemire and Bourget, 1996). At the community level, habitat complexity has been found to be positively correlated with beta diversity (Hewitt et al., 2005). Topographic features of the substratum (e.g. holes, cracks, pits and ridges) can, in fact, offer refuge from consumers and enhance habitat suitability for species with varying physiological requirements (Archambault and Bourget, 1996; Walters and Wethey, 1986), thus, creating small-scale gradients in diversity. In addition to topographic features of rocky bottoms, bioconstructions represent a further determinant of substratum complexity (Ballesteros, 2006). The structures edified by calcareous seaweeds or invertebrates generate secondary complex substrata that can enhance local diversity (Cocito, 2004; Gratwicke and Speight, 2005).

Anthropogenic perturbations can modulate the role of topographic complexity in shaping patterns of species distribution (Balata et al., 2007a). In coastal waters, the input of terrigenous sediments represents one of the major threats to marine biodiversity (Airoldi, 2003). High sediment loads have been demonstrated to alter the structure of benthic assemblages and to reduce species diversity (Airoldi, 1998; Airoldi and Cinelli, 1997; Gorgula and Connell, 2004). Sediment deposition, scouring and burial can damage susceptible organisms, causing a shift towards assemblages characterized by tolerant or opportunistic species (Airoldi, 2000; Balata et al., 2007b; Connell, 2005; Eriksson and Johansson, 2003; Irving and Connel, 2002; Piazzi et al., 2012; Schiel

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et al., 2006), with dramatic changes in morpho-functional groups dominating macroalgal assemblages (Balata et al., 2005, 2011). In addition, sediment deposition can erode both alpha and beta diversity of rocky habitats. Manipulative experiments have, in fact, shown that differences between assemblages on hard substrata differing in inclination were strongly reduced in areas subjected to high sediment deposition (Balata et al., 2007a).

Despite the large research effort investigating the ecological roles played by topographic complexity and high sedimentation, little is known about the interactive effects of these two factors in determining the structure of rocky benthic assemblages (but see Irving and Connel, 2002). Aiming to fill in this gap, we performed a three-year experimental study comparing the development of macroalgal assemblages among different combinations of substratum complexity (three levels of substratum complexity were considered: high, intermediate and low) and rates of sediment deposition (natural vs. high). In particular, we tested the following hypotheses: i) the structure of macroalgal assemblages (morpho-functional group composition and abundance) vary according to the topographic complexity of the substratum; ii) high sediment deposition reduces variations in the structure of assemblages among substrata characterized by a different complexity.

2. Material and methods

2.1. Study site

The study was performed between spring 2002 and late summer 2005 along the coast of Tuscany, south of the town of Leghorn (43°28′ 24″ N and 010°19′42″ E), on a rocky subtidal bottom, 12–15 m deep. At this site, rocky bottoms alternate with secondary substrata constituted by calcareous structures edified by Corallinales; both substrata are generally colonized by photophilous assemblages (Balata and Piazzi, 2008), but patches dominated by encrusting coralline macroalgae are common at depths shallower than 10 m (Bulleri, 2013); the invasive Chlorophyta, *Caulerpa cylindracea* Sonder (*ex Caulerpa racemosa* (Forsskål) C. Agardh var. *cylindracea* (Sonder) Verlaque, Huisman et Boudouresque, Belton et al., 2014) was patchily distributed at the site (Piazzi and Balata, 2008). The natural mean rate of sediment deposition has been evaluated between 3.1 and 52.4 g m⁻² day⁻¹ during 1 year period of sampling, with higher values in autumn and lower in summer (Airoldi and Virgilio, 1998).

2.2. Experimental design

In order to assess how high sediment deposition can alter the effects of substratum complexity on the development of macroalgal assemblages, artificial substrates of varying complexity were exposed to colonization by macroalgae under different levels of sediment deposition (natural or high). Three levels of substratum complexity were considered: high, intermediate and low. In order to generate realistic levels of complexity, encompassing the natural range found at the study site, $30 \times 21 \times 3$ cm concrete panels were built to simulate natural simple (e.g., urchin barrens, made of bare rock with a thin layer of encrusting calcareous Rhodophyta) or complex surfaces (e.g. coralligenous formations). Worth stressing is that our aim was not that of separating biological from physical effects of these surfaces on the structure of macroalgal assemblages. Topographic complexity was measured in eight 20 \times 20 cm plots for each type of complexity surface through the chain index, calculated as the ratio of the horizontal distance covered by a contoured chain to its stretched length (20 cm), in order to obtain values ranging from 0 to 1, with smaller values indicating increasing complexity (Grigg, 1994). An ANOVA performed on these complexity measures confirmed a significant (df = 1,14, F = 14.4, p = 0.002) higher complexity in bioconstruction (chain index = 0.72 ± 0.02 , mean \pm SE, n = 8) than in natural rocky surfaces (0.83 ± 0.04) . The complexity to be produced on artificial panels was estimated pressing a playdough on a randomly chosen area within each of the two types of habitats, to obtain a cast. A lattice copy of casts was made in the laboratory and used to produce each type of concrete blocks. In addition, completely smooth panels (hereafter referred to as Low complexity), from a cast of a smooth wooden surface, were built in order to generate a more comprehensive gradient of substratum complexity. Eighteen concrete panels were built for each complexity level, adding to a total of 54.

Eighteen areas, $\sim 4 \text{ m}^2$ and $\sim 15 \text{ m}$ away one from another, were then randomly identified at a depth of 12–15 m. Three randomly chosen areas were assigned to each of the 6 combinations obtained by crossing 3 levels of complexity (Low (L), Intermediate (I), High (H)) with 2 levels of sediment deposition (natural or high). Three replicate panels were then randomly fixed within each area by means of epoxy putty, after all organisms were cleared from a surface of about 1500 cm². In the areas assigned to high sediment deposition, sediments were added on each of the experimental units. Fine sediments (grain size $< 200 \,\mu m$) were collected on an adjacent shore and added at 30 day intervals. Each time, 400 g of sediments was manually deposited over each experimental unit (corresponding to an amount of about 211 g m⁻² day⁻¹). This amount was the same used in previous experiments (Balata et al., 2007a,b) and considered as a stressful condition for subtidal assemblages in this geographical area (Airoldi and Virgilio, 1998). In the case in which rough seas did not allow safe diving, addition of sediment was carried out as soon as sea conditions improved; this resulted in delays not greater than 2-3 days.

2.3. Sampling and statistical analyses

At the end of the study period, macroalgal assemblages were scraped off from experimental panels and preserved in 4% formalin seawater. Three years is a period of time sufficient for the development of mature assemblages, in our study system (Benedetti-Cecchi, 2000). In the laboratory, all macroalgal species were identified and the percentage cover of each species was evaluated on a grid and expressed as the percentage of the panel surface covered by spreading out algal thalli (Boudouresque, 1971).

Macroalgal species were divided in morphological groups (Appendix I) and the percentage cover of each group was calculated as the sum of the abundance of each species belonging to the group. Species were assigned to morpho-functional groups using an expanded classification based on thallus structure, growth form, branching pattern and taxonomic affinities; these morpho-functional groups have been shown to be sensitive to alterations in environmental conditions (Balata et al., 2011).

A permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001) was used to examine differences in the composition and abundance of morpho-functional groups among treatments. The analysis included the following factors: Substratum complexity (Low, Intermediate or High) and Sediment (natural or high) as fixed, crossed factor and Area (3 levels) as a random factor nested within the interaction Substratum × Sediment. The PERMANOVA was conducted on a Bray–Curtis dissimilarity matrix calculated from log(x + 1) transformed data. Prior to analysis, heterogeneity of variances was checked by means of PERMDISP (Anderson, 2006). This analysis showed that variation among replicates did not differ significantly across treatments (F = 3.807, P(perm) = 0.092). Pairwise tests were performed to compare levels of significant factors.

A principal coordinates analysis (PCO) was performed on a log(x + 1) transformed Bray–Curtis dissimilarity matrix (Anderson and Willis, 2003) in order to obtain a graphic representation of multivariate patterns. Finally, a SIMPER analysis (Clarke, 1993) was performed to identify the percentage contribution of each taxa/group to differences in Bray–Curtis dissimilarity among treatments.

Total percentage cover, species number, percentage cover of the main morpho-functional groups (1) prostrate, 2) filamentous and

Table 1

PERMANOVA comparing morpho-functional group composition and abundance among macroalgal assemblages on panels of different complexity (L = low complexity, I = intermediate complexity, H = high complexity), exposed to natural (=n) or high (=h) sediment deposition. Significant effects are in bold.

Source	df	MS	Pseudo-F	P(perm)
Substratum = Sub	2	383.1	10.97	0.377
Sediment = Sed	1	1765.6	50.58	0.002
$Sub \times Sed$	2	725.4	20.78	0.042
$Area(Sub \times Sed)$	12	349.0	30.67	0.001
Residual	36	113.7		
Total	53			
Pairwise test (Sub × Sed)	L, I: n L,I: h L, H: n L, H: n I, H: n I,H: h	P(MC) 0.896 0.589 0.021 0.230 0.092 0.329	L: n, h I: n, h H: n, h	P(MC) 0.037 0.168 0.018

3) larger-sized corticated Rhodophyta, 4) compressed, 5) filamentous uniseriate and 6) pluriseriate Ochrophyta, 7) filamentous uniseriate and 8) siphonous with thin compacted filaments Chlorophyta) and of *C. cylindracea* were analyzed by means of 3-way ANOVAs. Factors and levels considered in these analyses were the same as described for the multivariate analysis. Cochran's *C*-test was used before each analysis to check for homogeneity of variance (Underwood, 1997) and data were log(x + 1) transformed when necessary. Data were analyzed even when homogeneity of variances could not be achieved, as the ANOVA is robust for departure from this assumption when there are many independent replicates and sizes of samples are equal (Underwood, 1997). Results were, however, interpreted with caution, by judging the significance more conservatively ($\alpha = 0.01$). Student Newman Keuls (SNK) test was used for a posteriori multiple comparisons of means.

3. Results

A total of 106 macroalgal species were identified on experimental panels; among them, there were 13 Chlorophyta, 14 Ochrophyta and 79 Rhodophyta (Appendix I, electronic supplementary material). The main morpho-functional groups characterizing the assemblages were the siphonous Chlorophyta, with both compacted and separate



Fig. 1. PCO ordination. Hollow: natural levels of sediment deposition; filled: high levels of sediment deposition; triangles = low complexity, squares = intermediate complexity, circles = high complexity.

Table 2

Macroalgal taxa/groups	Mean R(%)	Mean R(%)	Contribution %
Filamentous Rhodophyta Erected corticated Rhodophyta Filamentous Chlorophyta	n-L 33.56 1.97 1.72	n-H 22.67 18.19 2.75	Dissimilarity = 47.74 44.96 40.73 5.69
Filamentous Rhodophyta Erected corticated Rhodophyta Filamentous Chlorophyta Caulerpa cylindracea	n-H 22.67 18.19 2.75 1.03	h-H 43.58 3.57 9.63 5.75	Dissimilarity = 50.50 46.12 27.49 13.99 8.38

filaments, filamentous pluriseriate and compressed Ochrophyta, filamentous and larger-sized corticated Rhodophyta, encrusting and articulated Rhodophyta.

The PERMANOVA showed a significant interaction between Substratum and Sediment (Table 1). Pairwise tests showed that sediment deposition influenced assemblage structure on H plates, but not on those characterized by lower complexity (L and I). Assemblages differed between L and H plates at natural levels of sediment deposition, but not when sediment deposition was high (Table 1). There was significant variability among areas.

The PCO showed that H plots segregated from the others at natural levels of sedimentation, while plots of different complexity were clumped together under high sedimentation regime (Fig. 1).

The SIMPER test showed that, at natural levels of sedimentation, differences between H and L plots were mostly due to a higher abundance of larger-sized corticated Rhodophyta in the former and filamentous Rhodophyta in the latter; differences between sedimentation levels in H plots were due to a higher abundance of larger-sized corticated Rhodophyta at natural levels of sedimentation and a higher abundance of *C. cylindracea* and filamentous Rhodophyta and Chlorophyta at high sedimentation regime (Table 2).

The ANOVA showed significant interactions between Substratum and Sediment for species number (Table 3), percentage cover of filamentous Rhodophyta, filamentous Ochrophyta and larger-sized corticated Rhodophyta (Table 4). SNK tests showed that, on H plates, species richness (Table 3, Fig. 2) and percentage cover of larger-sized corticated Rhodophyta (Table 4, Fig. 3) were higher at natural than high sediment deposition, while an opposite pattern emerged for filamentous Rhodophyta and Ochrophyta (Table 4, Fig. 3). The abundance of siphonous Chlorophyta with thin separate filaments was higher at high levels of sediment deposition, irrespective of substratum complexity (Table 4, Fig. 3). The percentage cover of the other main algal

Table 3

ANOVA comparing mean species number and total percentage cover of macroalgal assemblages on panels of different complexity (L = low complexity, I = intermediate complexity, H = high complexity), exposed to natural (= n) or high (= h) sediment deposition. Significant effects are in bold.

Source	df	MS	F	Р	MS	F	Р
		Species number			Percentage cover		
Substratum = Sub	2	771.7	15.63	0.002	174.3	0.23	0.844
Sediment = Sed	1	731.8	14.83	0.004	2519.6	33.43	0.082
$\operatorname{Sub} \times \operatorname{Sed}$	2	245.5	49.75	0.034	2035.6	2.70	0.100
$Area(Sub \times Sed)$	12	49.3	1.39	0.220	753.6	24.25	0.015
Residual	36	35.4			310.6		
Total	53						
Cochran's C							
SNK test (Sub \times Sed)		L: n = h	n: $L = I < H$				
		I: n = h	h: L = I = H				
		H: n > h					

Table 4

ANOVA on the abundance of the main morpho-functional groups of macroalgal assemblages on panels of different complexity (L = low complexity, I = intermediate complexity, H = high complexity) exposed to natural (= n) or high (= h) sediment deposition. Significant effects are in bold.

Source	df	MS	F	Р	MS	F	Р	
		Filamentous Rho	Filamentous Rhodophyta with prostrate filaments			Larger-sized corticated Rhodophyta		
Substratum = Sub	2	174.4	84.81	0.014	2127.9	12.61	0.002	
Sediment = Sed	1	375.6	18.26	0.002	220.9	13.09	0.273	
$Sub \times Sed$	2	365.4	17.76	0.002	976.8	57.89	0.019	
Area(Sub \times Sed)	12	20.5	1.55	0.146	168.7	16.28	0.105	
Residual	36	13.2			103.5			
Total	53							
Cochran's C		0.289	(n.s.)		0.265	(n.s.)		
SNK test (Sub \times Sed)		L: $n = h$	n: L = I = H		L: $n = h$	n: S = I < H		
		I: $n = h$	h: $L = I < H$		I: $n = h$	h: L = I = H		
		H: n < h			H: $n > h$			
		Smaller-sized file	Smaller-sized filamentous pluriseriate Ochrophyta			Filamentous uniseriate Chlorophyta		
Substratum = Sub	2	11,974.0	31.38	0.001	211.8	0.37	0.778	
Sediment = Sed	1	7273.05	190.66	0.001	6926.8	12.19	0.004	
$Sub \times Sed$	2	12,196.0	31.96	0.001	101.2	0.17	0.950	
Area(Sub \times Sed)	12	381.5	0.56	0.938	567.9	1.48	0.111	
Residual	36	674.1			383.2			
Total	53							
Cochran's C		0.289	(n.s.)		0.333	P < 0.01		
SNK test (Sub \times Sed)		L: n < h	n: L = I = H		SNK test (Sed)	n < h		
		I: n = h	h: $L = I < H$					
		H: n < h						

groups present in the studied assemblages, as well as total percentage cover, did not show significant differences among treatments.

The cover of the invasive Chlorophyta, *C. cylindracea*, was higher at natural than high sediment deposition on L plates, while an opposite trend was observed in H plots (Table 5, Fig. 4).

4. Discussion

Although there was generally high variability among experimental areas, high sediment deposition reduced differences between assemblages on substrata markedly differing in topographic features. Filamentous forms became the main component of macroalgal assemblages under high sediment deposition, although different filamentous groups responded differently to substratum complexity. These results suggest that this type of disturbance has the potential to homogenize biota, ultimately promoting dominance by algal turfs.

At natural levels of sediment deposition, greater substratum complexity promoted the development of assemblages dominated by architecturally complex species, such as erect corticated Rhodophyta, and enhanced species richness. Complexity of the substratum can favor macroalgae reproducing through the supply of spores from the water column by offering micro-habitats that, according to their abiotic and biotic features, can function as safe settlement sites (sensu Harper, 1977). For instance, the formation of turbulent eddies can enhance spores settlement both by concentrating them and reducing water speed in the proximity of the substratum (Foster, 1975; Johnson, 1994; Santelices, 1990). In addition, the accumulation of organic matter in pits or crevices could favor their germination (Santelices, 1990). At later stages, physical elements generating complexity (e.g., pits, holes, crevices) can reduce germling or juvenile mortality by lessening grazing pressure, either by providing refuges from herbivores or constraining their movements (Alexander, 2011; Benedetti-Cecchi and Cinelli, 1995; Bulleri et al., 2011; Vadas et al., 1992). On the other hand, complex substrata are more likely to retain greater amounts of sediments than more simple surfaces.

On complex substrata, erect species are competitively stronger than more opportunistic filamentous forms and can, thus, control their development. Such a competitive hierarchy between the two morphological groups of macroalgae was, however, altered under high sedimentation regimes. In fact, erect species decreased following the experimental sediment addition, being outcompeted by taxa constituting turfs such, as filamentous Rhodophyta and Ochrophyta and siphonous Chlorophyta with separate filaments. Deposited sediments can prevent settlement or germination of spores of architecturally complex species (Eriksson and Johansson, 2003, 2005). Also, scouring due to sediment particles can damage newly settled individuals or juveniles (Airoldi, 2003). Filamentous forms composing turfs are, in contrast, tolerant to both sediment burial and scour (Airoldi, 1998; Airoldi and Cinelli, 1997). Resistance of horizontal axes to the scouring of sediment particles, availability of spores throughout the year and vegetative propagation allow a quick recovery of space after disturbance (Airoldi, 2000). Indeed, sediment deposition, together with enhanced nutrient loading, is considered one of the major drivers of the shift in dominance from erect species to algal turfs, in urban areas (Balata et al., 2005,



Fig. 2. Species richness (A) and total percentage cover (B) of macroalgal assemblages (mean \pm SE, n = 9). Hollow: natural levels of sediment deposition; filled: high levels of sediment deposition. L = low complexity, I = intermediate complexity, H = high complexity. Asterisk indicates significant differences as shown by the SNK tests.



Fig. 3. Percentage cover (mean \pm SE, n = 9) of the main macroalgal morpho-functional groups. Hollow: natural levels of sediment deposition; filled: high levels of sediment deposition. L = low complexity, I = intermediate complexity, H = high complexity. Asterisk indicates significant differences as shown by the SNK tests.

2007a,b; Gorgula and Connell, 2004; Gorman and Connell, 2009; Irving and Connel, 2002; Tamburello et al., 2012).

Assemblages that developed on experimental panels of intermediate substratum complexity did not differ from those characterized by low complexity. This suggests that, irrespective of sediment deposition levels, a slight increase in complexity in respect to smooth surfaces was not sufficient to offset the competitive advantage of filamentous over erect species. Likely, attributes of physical elements generating small-scale topographic complexity (e.g., depth of pits and crevices; height of ridges), as well as their spatial heterogeneity, did not provide environmental conditions suitable for erect species to recruit or retain space at expenses of filamentous forms. In our study, the complexity of intermediate level panels was intended to mimic that of local, natural rocky surfaces. High sediment deposition would have little effect on macroalgal assemblages on these surfaces, since it is not the main driver of filamentous form dominance. More generally, the magnitude of negative effects of high sediment deposition on benthic macroalgal assemblages can be predicted to increase with increasing complexity of the substratum.

In particular, filamentous Rhodophyta achieved large percentage covers on both simple and intermediate complexity panels, regardless of levels of sediment deposition. Species within this group might play, therefore, a pivotal role in excluding erect species at low to intermediate levels of substratum complexity. This view is supported by the fact that other filamentous forms belonging to the Ochrophyta or Chlorophyta exhibited a clear positive response to the addition of sediments on all experimental panel types. Their abundance, although generally low (not exceeding ~15%), did not decrease from low/intermediate to high complexity panels, suggesting a weak interaction with erect species.

Different groups of erect macroalgae responded differently to the experimental enhancement of sediment deposition. The cover of largesize corticated Rhodophyta decreased under high sedimentation regime. In contrast, the cover of both compressed and corticated Ochrophyta and that of articulated Rhodophyta did not undergo major changes, confirming previous reports of these macroalgal groups being resistant to burial and scouring (Balata et al., 2007b).

A main ecological consequence of the loss of substratum-related differences between benthic assemblages can be a reduction of the beta-diversity (sensu Whittaker, 1972) of the system. In fact, the occurrence of small-scale variations in complexity of rocky bottoms can generate and maintain a patchy distribution of macroalgal assemblages, enhancing the beta-diversity of the system (Issa et al., 2014). A loss of beta-diversity implies widespread ecological homogenization, that is a marked simplification of the system, generally due to the decline of architecturally complex forms and dominance by opportunistic species (McKinney and Lockwood, 1999). This effect is to be considered particularly threatening in coastal ecosystems, since lower spatial variability can reduce the resistance of natural assemblages to stressors, potentially leading to more severe and irreversible changes (Olden et al., 2004).

An interesting finding of this study concerns the response of the invasive green seaweed, C. cylindracea, to experimental conditions. At natural levels of sediment deposition, the cover of C. cylindracea was smaller on high than intermediate complexity panels, while an opposite pattern emerged at high levels of sediment deposition. Substratum complexity has been shown to improve the spread of the alga favoring the anchoring of rhizoids and, consequently, the growth of stolons (Bulleri and Benedetti-Cecchi, 2008; Ceccherelli et al., 2002; Piazzi and Balata, 2009). Here, erect species likely outcompeted C. cylindracea from high complexity panels (Bulleri et al., 2010; Ceccherelli et al., 2002). Loss of erect species and dominance by algal turfs under high sedimentation rates favored the spread of the alga. Previous studies have shown that C. cylindracea is tolerant to sediment deposition (Piazzi et al., 2007) and that the complex three-dimensional matrix formed by algal turfs can foster the establishment and spread of the alga both by trapping sediment and minimizing the likelihood of being dislodged by waves (Bulleri and Benedetti-Cecchi, 2008; Bulleri et al., 2009; Piazzi et al., 2003).

Erect species played, however, no role in the decline of *C. cylindracea* on intermediate complexity panels following the increase in sediment

Table 5

ANOVA results on the abundance of *Caulerpa cylindracea* on panels of different complexity (L = low complexity, I = intermediate complexity, H = high complexity), exposed to natural (= n) or high (= h) sediment deposition. Significant effects are in bold.

Source	df	MS	F	Р
Substratum = Sub	2	365.0	27.80	0.072
Sediment = Sed	1	51.1	0.38	0.594
$\operatorname{Sub} \times \operatorname{Sed}$	2	3012.0	22.94	0.001
$Area(Sub \times Sed)$	12	131.2	0.91	0.555
Residual	36	143.2		
Total	53			
Cochran's C		0.321	(n.s.)	
SNK (Sed)		L: n = h	n:H < L < I	
		I: $n > h$	h: I < L < H	
		H: n < h		



Fig. 4. Percentage cover (mean \pm SE, n = 9) of *Caulerpa cylindracea*. Hollow: natural levels of sediment deposition; filled: high levels of sediment deposition. L = low complexity, I = intermediate complexity, H = high complexity. Asterisk indicates significant effects as shown by the SNK tests.

deposition. Indirect negative effects of sediments on filamentous forms are unlikely, since only filamentous Ochrophyta showed a modest increase in cover, following the addition of sediments. This suggests that the tolerance of *C. cylindracea* to high sediment deposition (Piazzi et al., 2005, 2007) would vary according to substratum complexity. Neutral to negative effects at low to intermediate substratum complexity versus positive effects at high substratum complexity may indicate that differential accumulation patterns and retention of sediments may ultimately determine the response of the seaweed to this physical stressor.

5. Conclusions

The study shows that increases in sediment deposition can reduce variations in the structure of macroalgal assemblages among substrata characterized by different complexity, with consequent reduction of both alpha (i.e., loss of species) and beta diversity (i.e., decreased small-scale variation in community structure). In addition, although not quantified in the present study, the decline of architecturally complex macroalgae may result in the alteration of associated sessile and mobile invertebrate assemblages (Chemello and Milazzo, 2002). In addition, our study suggests that high sediment deposition may foster the success of opportunistic invaders, which, once established, can trigger positive feed-backs (e.g., sediment retention in the case of *C. cylindracea*) that prevent the system to recover (Bulleri et al., 2010). High sediment deposition and invasion may ultimately result in widespread biotic homogenization, with severe consequences on the functioning and the ecological properties of the system (Olden et al., 2004).

The results of our study are relevant for the management of marine biodiversity in future climate change scenarios, since human-driven modifications in precipitation regime (i.e., enhanced frequency of extreme rain events and floods), may increase sediment supply to coastal areas. Enhanced sedimentation, along with ocean acidification (Russell et al., 2009), is likely to promote the dominance of benthic assemblages by filamentous forms, reducing beta-diversity. Thus, controlling inputs of sediment deposition through large-scale management of hydrographic basins, may sustain physical and biological mechanisms that promote biodiversity in marine coastal systems, mitigating detrimental effects of ocean acidification.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at http://dx. doi.org/10.1016/i.jembe.2015.03.005.

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