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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).

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 × 21 × 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 × 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 ± 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, ~4 m^2 and ~15 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 cm^2. In the areas assigned to high sediment deposition, sediments were added on each of the experimental units. Fine sediments (grain size < 200 μm) 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