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Concomitance of oligotrophy and low grazing pressure is essential for the resilience of Mediterranean subtidal forests

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ABSTRACT

The study aimed at investigating factors influencing the recovery of the canopy seaweed *Cystoseira brachycarpa*. A manipulative experiment was done to test if in barren patches the recovery of *Cystoseira* I) is enhanced by the removal of the urchins, II) is prevented by eutrophication, III) depends on the time of patch clearance and IV) decreases with the distance from *Cystoseira* bed edge within the barren patch. The effects of the same factors on the structure of the macroalgal assemblage were also tested. *Cystoseira* recovered abundantly only in clearings where nutrients were not added and urchins were removed. Furthermore, *Cystoseira* recovered irrespectively of the time the patches were cleared and the distance from the canopy edge. This study showed that the lack of sea urchins at oligotrophic conditions was essential for *Cystoseira brachycarpa* recruitment, providing evidence that interacting constraints are involved in the recovery of *Cystoseira* beds.

1. Introduction

Foundation species have long been recognized as facilitators of a whole community of organisms through habitat creation (Bertness and Callaway, 1994; Ellison et al., 2005). Kelps, conifers, and corals, for instance, are spatially dominant organisms whose biogenic structure promotes species coexistence through the amelioration of physical stress and the creation of fine-scale, complex matrices in which smaller organisms find refuge from predators and competitors (Jones et al., 1994; Bruno and Bertness, 2001), contributing to increase biodiversity (Graham, 2004). Thus, the conservation of habitat-forming species is a crucial goal for ecologists and environmental managers, in order to maintain biodiversity and ecosystem services. Habitat-formers are normally long-living organisms that in some cases exhibit low recruitment rates (Åberg, 1992). These slow-growing species are highly vulnerable to human-induced alterations and recruitment represents a critical process to determine the resilience of these systems (Schiel and Foster, 2006).

In marine systems, canopy macroalgae, mainly belonging to Laminariales and Fucales, are among the most important habitat-forming organisms (Airoldi and Beck, 2007). In fact, biogenic habitats constituted by macroalgae are considered one of the most relevant ecosystem of temperate rocky coasts in terms of extent, production and biodiversity (Steneck et al., 2002). Most canopy-forming macroalgae are sensitive to human disturbance and a worldwide decline of macroalgal beds has been reported during the last decades (Steneck et al.,

2002; Eriksson et al., 1998, 2002). The causes of this loss mostly include urbanization, mechanical destruction of coasts, introduction of alien species and decreased of water quality as a consequence of pollution and enhanced sediment loads (Soltan et al., 2001; Airoldi, 2003; Connell, 2005; Schiel et al., 2006). Overgrazing by sea urchins has been described to cause the shift from canopy macroalgal beds to barrens dominated by encrusting Corallinales (Pinnegar et al., 2000; Shears and Babcock, 2003). Barrens, widespread in temperate rocky habitats (Sivertsen, 2006; Hernandez et al., 2008; Perreault et al., 2014; Ling et al., 2015), are considered an alternative stable state of algal beds (Filbee-Dexter and Scheibling, 2014). The knowledge of mechanisms driving shifts between the two states is crucial to allow the maintenance and/or the recovery of algal beds (Hereu et al., 2008).

In the Mediterranean Sea the most important canopy-forming macroalgae are species of the genus *Cystoseira*. Most of Mediterranean species of *Cystoseira* are endemic and they represent the dominant assemblages of shallow subtidal rocky habitat (Sales and Ballesteros, 2010; Sales et al., 2012; Cheminée et al., 2013). *Cystoseira* are among the largest Mediterranean algae and play a relevant ecological role (Sales and Ballesteros, 2012). The Action Plan for the Conservation of Marine Vegetation in the Mediterranean Sea, within the framework of the Barcelona Convention, identifies the conservation of *Cystoseira* belts as a priority (RAC-SPA., 2000). *Cystoseira* beds are locally extinct or extensively regressed due to human pressure (Rodríguez-Prieto and Polo, 1996; Munda, 2000; Thibaut et al., 2005, 2015; Mangialajo et al., 2008; Sales et al., 2011). Maintaining populations of habitat-forming

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species depends on the resistance of populations to stress and on their ability to recover after disturbance. Most studies focused on the decline of macroalgal beds (Bulleri et al., 1999; Benedetti-Cecchi et al., 2001), while little attention has been paid to mechanisms allowing the recovery of *Cystoseira* assemblages (Perkol-Finkel and Airoidi, 2010).

Overgrazing by the sea urchin *Paracentrotus lividus* (Lamarck, 1816) related to overexploitation of predator fishes has been described as a main cause of barren formation (Guidetti et al., 2003; Guidetti and Dulcic, 2007; Gianguzza et al., 2011; Giakoumi et al., 2012). However, in many Marine Protected Areas no *Cystoseira* recovery has been reported to occur, even after the re-establishment of natural predator-prey interactions (Micheli et al., 2005; Bevilacqua et al., 2006; Cardona et al., 2007). This evidence supports the hypothesis that multiple factors might be involved in the algal recovery and that resilience of the habitat is determined by complex mechanisms. Among these factors, intraspecific interactions with the adults, competitive interactions with turf-forming algae, availability of nutrients and grazing by herbivores can be pivotal determinants of the recovery of these subtidal forests (Benedetti-Cecchi and Cinelli, 1992; Valentine and Johnson, 2005; Bonaviri et al., 2011; Guarnieri et al., 2014).

In the Mediterranean Sea, barrens are stabilized by the maintaining effect of both the sea urchin *Arbacia lixula* (Linnaeus, 1758) and the limpet *Patella caerulea* Linnaeus, 1758 (Bulleri et al., 1999; Bonaviri et al., 2011; Bulleri, 2013; Piazzì et al., 2016) that prevent the recovery of algal turfs. However, little is known about the *Cystoseira*-barren transitions, although mosaics of barren and vegetation patches are very common, as they usually are the result of sea urchin grazing (Agnetta et al., 2015) around the refuges (rock crevices) (Benedetti-Cecchi et al., 1998; Bulleri et al., 1999, 2002).

The aim of this study is to investigate whether the fate of the barren patches mixed to patches of *Cystoseira* depends on the herbivore pressure (sea urchin density) and nutrient regime that were manipulated in the field. Therefore the experiment was done to test if in barren patches the recovery of *Cystoseira* I) is enhanced by the removal of the urchins, II) is prevented by eutrophication, III) depends on the time of patch clearance and IV) decreases with the distance from *Cystoseira* bed edge within the barren patch. The effects of the same factors on the structure of the macroalgal assemblage were also tested. Results would provide important insights to predict *Cystoseira* recovery and to address efforts promoting the resilience of the alga.

2. Methods

This study was done in an oligotrophic site of the North Western Sardinia (Western Mediterranean Sea, 43° 03' 09" N, 08° 56' 15" E) characterized by rocky platforms about 15 m deep. In this site, large *Cystoseira brachycarpa* J. Agardh beds are interspersed to barren areas (1–5 m² in size) of encrusting corallines. Inside *Cystoseira* beds, eight patches 4 m² wide were cleared from all erect and turf macroalgae on each time: April 2015 (Time 1) and July 2015 (Time 2). Two times of clearance were chosen to test the hypothesis that the recruitment of *Cystoseira* was constrained by the stage of development of the macroalgal assemblage. Clearance of patches was performed removing all erect and turf algae by scraping the substrata through a wire brush and paying attention that none of the portions of thalli were left, simulating the barren due to *P. lividus* overgrazing.

Nutrient availability (ambient and enriched, N– and N+) and sea urchin density (control and removed, H+ and H–) were manipulated and each condition (N–H–, N–H+, N+H–, and N+H+) was assigned to two patches for each clearing time. Patches were at least 5 m distant from each other and in each patch, four plots (400 cm² in size) were selected at the edge and four at the centre (> 70 cm far from the edge).

The number of *Arbacia lixula* was adjusted to 0 and 5 individuals m⁻² in H– and H+, respectively, reproducing the natural density measured in the barren areas (4.6 ± 0.3, mean ± SE, n = 12

replicated quadrats of 1 m²), and maintained by means of monthly visits adding or removing individuals within the patch. The use of *A. lixula* was preferred to that of *P. lividus* because the former is considered capable to maintain barren state (Bonaviri et al., 2011; Bulleri, 2013) and it is strictly associated to habitat dominated by Corallinales while *P. lividus* grazes on fleshy macroalgae (Agnetta et al., 2015). In fact, throughout the study period, variations in sea urchin density in experimental patches were absolutely negligible.

Nutrient enrichment was obtained through 20 × 5 × 5 cm nylon mesh bag (1 mm mesh size), containing 150 g fertilizing pellets (Piazzì et al., 2011). Mesh bags were fixed (by using cable ties) to tiles cemented to the substratum. The composition of the pellets (Osmocote®, Scotts) was a combination of nitrogen (15%, made up of 7% ammonia and 8% nitrate), phosphorus (9% in the form of P₂O₅) and potassium (9% as KNO₃). Every two months, before the complete dissolution of pellets, the bags were replaced in order to maintain water nutrient concentration high throughout the study period. To verify the effectiveness of experimental fertilization, concentration of seawater nutrients was measured on three patches selected at random among those with and without nutrient addition. Samples were filtered (0.45 µm filter size) and analysed using a continuous-flow AA3 Auto-Analyzer to determine the seawater concentration (mg l⁻¹) of ammonia (N-NH₄⁺), nitrite (N-NO₂⁻), nitrate (N-NO₃⁻) and phosphorus (P-PO₄³⁻). Both total dissolved inorganic N and P concentrations were significantly higher (F_{1,4} = 1368.2 and F_{1,4} = 1005.9 respectively for N and P, both p < 0.01, in ANOVA analyses, Underwood, 1997) in nutrient-enhanced boulders rather than in controls.

To estimate changes in algal cover, plots were photographically sampled in July 2015, October 2015, April 2016, July 2016 and October 2016. Photographs were analysed in the laboratory to evaluate the percent cover of the main macroalgal taxa/morphological groups. Sample areas were divided into 25 sub-squares and the percent cover in each sub-square was visually estimated by assigning each species a score ranging from 0 (species absent) to 4 (100% cover), then summing scores across the 25 sub-squares (Dethier et al., 1993).

The percent cover of the main taxa/morphological groups obtained in October 2016 was analysed by 5-way ANOVAs, with the factors Herbivory (herbivores present H+ vs herbivore absent H–), Nutrient (nutrient ambient N– vs nutrient enhanced N+), Time (Time1 vs Time2) and Distance from adults of *Cystoseira* (edge vs centre of the patch) fixed and orthogonal, while the factor Patch (two levels) was random and nested within the interaction Nutrient × Herbivory × Time. Cochran's C-test was used before each analysis to check for homogeneity of variance (Underwood, 1997) and data were transformed when necessary. Student Newman Keuls (SNK) test was used for a posteriori multiple comparisons of means.

3. Results

Cystoseira brachycarpa recruits started to be appreciable in April 2016. The alga recruited abundantly only at one combination of nutrient × herbivore, in clearings where nutrients were not added and urchins were removed (N–H–), irrespectively of the distance from the canopy edge and the time that patches were cleared (Fig. 1a, Table 1). At all other conditions (N+H+, N+H– and N–H+) *C. brachycarpa* was found only occasionally and its canopy cover remained irrelevant throughout the whole study period. Significant differences between patches were also highlighted (Table 1).

At the end of the study period, the fleshy macroalgae were about 70% of the cover in N–H– as well as in N+H+; furthermore, they totally covered the N+H– plots, while they were nearly absent in N–H+. No significant differences between clearing times were detected (Fig. 1b, Table 1).

Halopteris scoparia (Linnaeus) Sauvageau, *Padina pavonica* (Linnaeus) Thivy, encrusting corallines and turf algae were the main taxa/groups of the assemblage and they responded differently to the experimental

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