



Mediterranean sponges from shallow subtidal rocky reefs: *Cystoseira* canopy vs barren grounds

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ABSTRACT

Porifera richness was investigated in *Cystoseira* canopies vs barren grounds considering different substrates at 6 areas in the Central-Western Mediterranean Sea. In total 31 sponge taxa were recorded at 2–7 m depth and the sponge community structure and composition were characterized by a notably low richness with 25 taxa in the *Cystoseira* forest and 15 in the barren area. As for the sponge habitus, the massive sponges were dominant in both facies, whereas encrusting, and cavity dwelling sponges were found in higher numbers in the *Cystoseira* forest. Results revealed that rocky substrata seem to play a key role in driving the sponge community composition and diversity in both facies. In this work we explore the role of *Cystoseira* canopy as a suitable facies for sponges. Sponge assemblages were persistent, strongly resilient in space occupation and consequently support stability in both facies. Some species seem to be pre-adapted to live under the sub-optimal conditions of the barren grounds, i.e. the absence of the *Cystoseira* fronds shelter. This focus on sponge successful eco-etological performances in 'submarine deserts' such as barren areas shows features as shown in a few other sessile benthic invertebrates.

1. Introduction

Temperate subtidal rocky systems are usually dominated by seaweed assemblages inhabited by a diversified fauna which rely on macroalgae for shelter, recovery, food and settlement (Beckley, 1982; Coull et al., 1983; Carr, 1989). Algal canopies are key habitat formers in shallow subtidal and intertidal zones of rocky shores (Reed and Foster, 1984; Santelices and Ojeda, 1984; Dayton, 1985; Duggins and Dethier, 1985; Benedetti-Cecchi and Cinelli, 1992). Macroalgal stands affect understory assemblages by modifying physical factors such as levels of light (Reed and Foster, 1984), water movement (Duggins et al., 1990), desiccation (McCook and Chapman, 1991), and by sweeping the substratum through the movement of the fronds (Velimirov and Griffiths, 1979; Hawkins, 1983). However, it is well known that this productive and well diversified seaweed assemblage can suddenly switch to impoverished facies dominated by encrusting organisms i.e. barren grounds defined firstly as “Isoyake” *sensu* Okamura and Tago (1915) meaning ‘marine desert’ (Costa et al., 2016).

In the Mediterranean Sea, the so called “*Cystoseira* forest” is one of the most common photophilous communities, with canopy forming algae, in the infralittoral rocky coasts. This biotope was firstly reported

by Pérès and Picard (1964) and the earliest studies focused on the faunal structure of *Cystoseira* facies were carried out by Bellan-Santini (1969) and Boudouresque (1969). More recently, several studies investigated in depth the structure and dynamics of this fragile biotope (Ballesteros, 1988, 1990; Benedetti-Cecchi et al., 2001; Fraschetti et al., 2001; Cheminée et al., 2013; Mangialajo et al., 2013; Capdevila et al., 2016). One of the most impacting activities on the stability of such living community is the sea urchin grazing performed in the Mediterranean Sea almost exclusively by *Arbacia lixula* (Linnaeus, 1758) and *Paracentrotus lividus* (Lamarck, 1816) (Bulleri et al., 1999). Their aggressive feeding, in several cases, determines the algal canopy disappearance, transforming it into an underwater bare rocky desert, called “barren” (Ling et al., 2015).

The key role of sea urchins in driving the shift between the forest state characterized by complex seaweeds assemblages and the barren state dominated by encrusting coralline algae was investigated by Sala et al. (1998). At high densities (7–20 ind./m²), *P. lividus* has a bulldozing effect on *Cystoseira* spp. forest, leading to the formation of barren areas (Kempf, 1962; De Verlaque, 1987; Agnetta et al., 2015). On the other hand, grazing of *A. lixula* is crucial for the barren grounds persistence (Benedetti-Cecchi et al., 1998; Palacín et al., 1998; Bulleri et al., 1999;

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Guidetti and Dulčić, 2007; Bonaviri et al., 2011). The reduction of predation or harvesting of sea urchins can allow the increase of their abundance and indirectly the shift towards the barren state (Shears and Babcock, 2002; Steneck et al., 2002; Hill et al., 2003; Konar and Estes, 2003; Gagnon et al., 2004; Knowlton, 2004; Wright et al., 2005; Bonaviri et al., 2009). The barren condition persists over time even after the subsequent decrease in the urchin densities (Privitera et al., 2008).

The transition from complex erect seaweeds assemblages to the barren state is expected to result in large-scale changes in community structure and ecosystem functioning and to have detrimental effects on fauna (Steneck et al., 2002). However a recent study revealed that barrens support a rich cryptic invertebrate community, composed mainly by spionids and sipunculids in the Aleutian Archipelago (Chenelot et al., 2011). In this regard, it was proposed that crevices and interstices produced by the action of encrusting algae on substrata are suitable for colonization processes by bryozoans, polychaetes, molluscs, and other invertebrates (Chenelot et al., 2011). Some species, referred to as keystones (*sensu* Paine, 1969) or engineering species (*sensu* Jones et al., 1994), are fundamental to the production and maintenance of distribution and abundance patterns of other organisms. Their strong effects on other organisms and on the habitat can be explained in terms of the physical features modification and direct and indirect influence on biotic interactions.

The Mediterranean sponge fauna is globally one of the best documented (Hooper and van Soest, 2002; Pansini et al., 2011; Van Soest et al., 2017) and it is an essential component of benthic communities with approximately 720 species (Pansini and Longo, 2003; Van Soest et al., 2017). Sponges are among the most common, abundant, and diversified faunal taxonomic groups in Mediterranean coastal sciaphilous communities such as coralligenous ($n > 300$; Bertolino et al., 2013; Longo et al., 2017) and caves ($n > 300$; Cadeddu, 2012; Gerovasileiou and Voultsiadou, 2012) while are less plentiful in photophilous biocoenosis such as *Posidonia* meadows ($n < 50$; Pansini and Pronzato, 1985; Padiglia et al., 2015) and in subtidal areas ($n = 25$; Pansini et al., 2000). Furthermore, sponges are a key component of rocky reef communities and they may play significant ecological roles such as benthic-pelagic coupling, food source, and provision of habitat for other organisms in these systems (Bell, 2008).

Considering the potential effect of erect algae on the assemblage structure in temperate rocky reefs, we investigated the composition and taxonomic richness of sponges in two contrasting habitats (facies): the *Cystoseira* forest and the barren grounds. This presents a good opportunity to compare sponge communities in these Western-Central Mediterranean biotopes in an area with a global distance of approximately 1500 km, between 4th and 18th longitude meridians East i.e. East/West Mediterranean transect tracking the eastern Adriatic Sea, the Tyrrhenian Sea, the North Sardinian Sea, and the Balearic Sea. Data on sponges inhabiting these shallow subtidal rocky reefs are few and scattered in the literature (Pulitzer-Finali and Pronzato, 1980; Frascchetti et al., 2006). Therefore, the Porifera dataset was used to investigate any differences between the two facies and to test the following hypotheses: i) the two facies do not diverge significantly for the number of taxa (taxonomic richness), the sponges habitus, and the percentage of sponge coverage vary in the two facies depending on the study area; ii) the geological nature of the rocky substratum and the biogeographic patterns of the local sponge fauna do not constrain the taxonomic richness and the percentage of sponge coverage in the two facies.

2. Material and methods

2.1. Sampling

Samples were collected from six areas in the Western-Central Mediterranean Sea (Fig. 1) during June–July 2014 on rocky reefs at

2–7 m depth. Sponge abundance and diversity was quantified in both facies (*Cystoseira* canopy and barren ground). For each of the six areas we sampled two sites with three replicates per experimental cell for erect algae canopy and two for barren ground by scraping the entire rocky substrate community within 20 × 20 cm quadrats (Gambi and Dappiano, 2003). The collected material was fixed in formalin and sorted in the laboratory (LM, stereomicroscopy). Sponge specimens and/or their fragments were processed according to standard methods for the preparation of slides and identified to species level focusing on macro- and micro-diagnostic morphotraits of skeletal silica and/or spongin components (LM, transmitted light microscopy). The samples were stored in a reference collection deposited at the DISTAV-University of Genoa. The status of taxa was validated on the basis of *Systema Porifera* (Hooper and van Soest, 2002), *Fauna d'Italia* (Pansini et al., 2011; Pronzato and Manconi, 2011) and the World Porifera Database (Van Soest et al., 2017).

2.2. Statistical analysis

Coverage percentage was studied through univariate comparison between two factors, areas (6 levels) and substrates (4 levels). Since data did not meet ANOVA assumptions for both factors, the non-parametric Kruskal-Wallis test was used to test any difference in terms of coverage between substrates and areas. Species abundance was analysed through TwoWay Permanova (Anderson and Walsh., 2013), with substrate (4 levels) and facies (2 levels) as factors in order to test for differences in species composition and abundances between sampling facies (CYS and BAR) and among substrates. The SIMPER (Similarity Percentage) test (Clarke, 1993) was used to evaluate the taxa morphology that contributes most to the differences between conditions. A multivariate non Metric-Multidimensional Scaling (Bray-Curtis similarity) was used to illustrate the relationships between facies and sponge species assemblage.

3. Results

The environment observed in the two facies was peculiar to each site, but in general *Cystoseira* spp. frondose algae form canopy in all studied areas, and barren ground was shaped by rocky stretches where coralline algae with organisms resistant to pasture by sea urchins.

3.1. *Cystoseira* canopy

The *Cystoseira* canopy recorded in the six areas revealed the presence of a Porifera community with 25 taxa (Table 1). The dominant habitus of the sampled sponges ranged from massive (14 species) to thickly or massively encrusting (5 species), cavity dwelling (3 species), and boring (1 species) (Table 1). Massive sponges were dominant in four out of the six areas, while in Menorca the encrusting habitus is dominant (Fig. 2A). The recorded species richness values were low i.e. Adriatic Sea (Croatia, $n = 8$; Montenegro, $n = 6$), Tyrrhenian Sea (Ustica and Capraia, $n = 5$), Balearic Sea (Menorca, $n = 4$) and Sardinian Sea (Sardinia, $n = 1$). An important point is the presence of the rare *Darwinella gardineri* Topsent, 1905 in *Cystoseira* canopy at the Ustica Island. This is the second Mediterranean record of this inconspicuous yellow dendroceratid species characterized by thinly encrusting growth form in small patches (Pronzato, 1975).

3.2. Barren

A total of 15 sponge taxa were recorded in the barren of the six areas (Table 1). The habitus of sponges ranged from massive (10 species), thinly to thickly encrusting (2 species), and boring (2 species) (Table 1). Massive sponges were dominant in four out of the six areas. Encrusting sponges were dominant in Menorca (Fig. 2B). The recorded species richness values were low i.e. Adriatic Sea (Croatia, $n = 10$; Montenegro,

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