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The role of Mediterranean sponges in benthic-pelagic coupling processes: *Aplysina aerophoba* and *Axinella polypoides* case studies



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ABSTRACT

Sponges are important components of marine benthic communities with a worldwide distribution ranging from polar to tropical regions. They play a key role in benthic-pelagic coupling processes through their active suspension feeding, providing a trophic link between the benthos and the overlying water column. Little is known about their broad-scale distribution and feeding ecology. The general tendency is to quantify their trophic impact through small patch estimations. In this work, two of the most abundant sponges in Mediterranean coastal bottoms (Aplysina aerophoba and Axinella polypoides) were studied combining remotely operated vehicle (ROV) survey with in situ feeding experiments. Spatial, bathymetrical distribution and population size structure of these species were analysed, together with their trophic ecology, in spring and autumn. We found that A. aerophoba is distributed between 5 and 20 m depth, with maximum densities of 1.6 sponges m^{-2} . This species ingested 0.12–0.39 mg of carbon (C) g AFDW⁻¹ (ash free dry weight) day⁻¹ in spring and 0.09–0.13 mg C g AFDW⁻¹ day⁻¹ in autumn. Conversely, *A. polypoides* was found between 10 and 70 m depth, with maximum densities of 7.6 sponges m $^{-2}$. This species ingested 0.07–0.17 mg C g AFDW $^{-1}$ day $^{-1}$ 1 in spring, and 0.18–0.60 mg C g AFDW⁻¹ day⁻¹ in autumn. The highest uptake of C concentrated between 5 and 15 m depth for A. aerophoba and between 65 and 70 m depth for A. polypoides. In the 1.14 ha of studied coastal bottom, A. aerophoba ingested 1.87 g C during spring and 0.19 g C during autumn, whereas A. polypoides 13.60 g C and 29.36 g C during spring and autumn, respectively. The present approach allowed a spatially explicit quantification of benthic-pelagic coupling processes produced by two of the most common sponges in a Mediterranean coastal area. This methodology, applied to benthic communities, mirrors similar approaches used in terrestrial forestry studies for C flux estimation.

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1. Introduction

Sponges (Porifera) have been important components of benthic fauna since the Early Cambrian (Zhang and Pratt, 1994). There are more than 8000 known species (World Porifera Database; www. marinespecies.org/porifera; Van soest et al., 2014) distributed worldwide in marine and freshwater systems (Hooper and Van Soest, 2002). These metazoans became dominant during climate change shifts, forming transitional reefs that substituted calcium carbonate bioconstructions (Copper, 1994).

Sponges play different functional and structural roles (Bell, 2008), either bio-eroding or consolidating substrata, providing protection from predation and enhancing survival of associated species, thus increasing biodiversity (Marliave et al., 2009). They represent important carbon (C) sinks, accumulating biomass in three-dimensional or

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encrusting long-lived structures (Maldonado et al., 2012), and play an important role in the biogeochemical cycles of C, nitrogen (N) or silicon (Si) (Nixon et al., 1976; Richter et al., 2001; Maldonado et al., 2005; de Goeij et al., 2008). Although sponges can use food sources ranging from dissolved organic matter (DOM) (de Goeij et al., 2008) to small crustaceans (<1 mm) (Vacelet and Boury-Esnault, 1995), they primarily feed on picoplankton (<2 μ m) with efficiencies up to 99% (Pile et al., 1996; Ribes et al., 2005).

The C transfer from pelagic to benthic systems has been estimated in shallow (Ribes et al., 1999a; Ribes et al., 2005) and deep environments (Pile and Young, 2006; Yahel et al., 2007; Kahn et al., 2015). However, most studies have quantified the C captured per m⁻² only on small patches (Rossi et al., 2004) and substantial work is still needed to quantify the influence of sponges in benthic-pelagic coupling and biogeochemical cycles on a broad spatial scale. If these estimates are coupled with species distribution, density and population structure data over large areas, the impact of the sponge feeding can be quantified at the ecosystem-level. This approach is commonly used in landscape ecology (Bekkby et al., 2002) to infer the

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role of forests, crops or grasslands as C sinks. This approach might help to bridge the gap of knowledge in between landscape and seascape ecology (Pittman et al., 2011).

Here we study the role in benthic-pelagic coupling processes of two of the most common Mediterranean coastal sponges, Aplysina aerophoba (Nardo, 1833) (Orden: Verongida, Family: Aplysinidae) and Axinella polypoides Schmidt, 1862 (Order: Halichondrida, Family: Axinellidae) (Fig. 1). The two species inhabit different communities and show a different morphology, feeding and physiological strategy; the first is characteristic of Mediterranean photofilic algae and precoralligenous communities, whereas the second is among the main constituents of the coralligenous community (Ballesteros, 2006; Gili et al., 2014). A. aerophoba is a massive species, organized in chimney-like structures with high symbiotic microbial abundance (HMA), which is partially constituted by photosynthetic cyanobacteria (Vacelet, 1970). A. polypoides is an erect, tree-like sponge with low microbial abundance (LMA). The microbial density in the tissues of HMA sponges is 2 to 4 orders higher than that of the surrounding water (Vacelet and Donaday, 1977; Friedrich et al., 2001). Conversely, for LMA species, it is the same as in the surrounding water (Hentschel et al., 2003). Different densities of bacteria in the sponge tissue contribute to determine the distribution pattern of the species as well as its clearance rates and feeding strategy (Vacelet and Donaday, 1977; Friedrich et al., 2001), depending on the phototrophic contribution of endosymbiotic bacteria or algae (Wilkinson, 1983).

Based on Coppari et al. (2014), quantitative analysis of video transects performed by a remotely operated vehicle (ROV) were coupled to data from in situ feeding experiments to estimate the trophic impact and the C flux mediated by these coastal Mediterranean sponges over a large extent. ROV surveys allow to determine the abundance and distribution pattern of megabenthic species over large areas and depths that cannot be sampled by SCUBA diving (Mortensen and Buhl-Mortensen, 2004; Gori et al., 2011a), and where several benthic suspension feeders are often the most abundant organisms (Rossi et al., 2008; Bo et al., 2011; Gori et al., 2011a; Ambroso et al., 2013; Coppari et al., 2014). In situ experiments enable the determination of the feeding habits of benthic suspension feeders under natural conditions (Ribes et al., 1999b; Tsounis et al., 2006) taking into account seasonal changes in food availability and retention rates (Ribes et al., 1998).

This study was consequently organized as follows: (1) characterize the spatial distribution pattern of *A. aerophoba* and *A. polypoides* over a broad geographical and bathymetrical extent; (2) describe their population size structure; (3) perform in situ experiments to quantify the feeding habits and C uptake of the two species in spring and autumn and to test the effect of the seasonality; and (4) estimate the total

amount of C ingested by the studied species and how it changes with depth over the entire study area.

This study will increase our understanding of the distribution pattern of two important sponge species of the Mediterranean coastal bottoms, and will provide quantitative data about their role in benthic—pelagic coupling processes.

2. Methods

2.1. Study area

Fieldwork was performed in Cap de Creus (42° 19′ 12″ N; 003° 19′ 34" E) on the northern extreme of the Catalan Coast (northwestern Mediterranean Sea), bordering France. The study area was sub-divided into 7 subareas, from A to G (see also Gori et al., 2011a) according to the main hydrodynamic patterns in the zone, and the specific features of the studied coast (Fig. 2). The general circulation pattern is characterized by the dominance of the Liguro-Provençal-Catalan current (or Northern current), which flows south-westward creating an east-to west circulation (DeGeest et al., 2008). The study area receives sediment inputs from the northern Gulf of Lions (Durrieu de Madron et al., 2000), especially by the Rhone River that supplies ~90% of the total freshwater in the gulf (Palangues et al., 2006). The most important winds influencing the study area are the northerly Tramuntana and the northwesterly Mistral that occur for 41% and 28% of the time, respectively. Strong south-easterly and easterly marine winds are rare (<6% of the time) and brief (less than 3 days), in contrast to the northerly ones that can last up to one month (Ulses et al., 2008). Consequently, subarea A is the most sheltered area of the surveyed coast; subareas B, C, D are affected mainly by easterly winds and are not directly influenced by the main near-bottom currents (Ulses et al., 2008; DeGeest et al., 2008). Subareas E and F are directly exposed to the main winds and wave actions in the study area (Ulses et al., 2008), as well as to the main near-bottom currents which accelerate around the cape (DeGeest et al., 2008). Due to the reduced influence of the main near-bottom currents, subarea G is characterized by sediment deposition processes.

2.2. Sponge distribution and size structure

2.2.1. Sampling procedure

Fieldwork was conducted in October–November 2004. Video transects were performed with the ROV Phanthom XTL equipped with a SONY FCB S3000P 3CCD camera (with a resolution of 700 horizontal lines), a depth sensor, a compass, and two parallel laser beams that provide the scale to define a fixed width of the transects (0.5 m) for

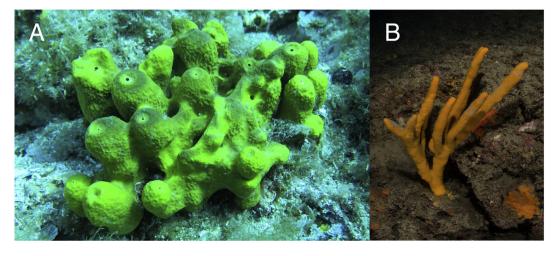


Fig. 1. Sponge species investigated in this study: *Aplysina aerophoba* (A), and *Axinella polypoides* (B). Photos by Núria Viladrich and Federico Betti.

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