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Planktonic prokaryote and protist communities in a submarine canyon system in the Ligurian Sea (NW Mediterranean)

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ABSTRACT

Submarine canyons are large geomorphological features that incise continental margins and act as highly dynamic conduits of sediments from shallow to the deep-sea regions. They are often regarded as biodiversity and biomass hotspots, but their role in influencing plankton communities is still poorly known. We studied the ecology of planktonic deep-sea microbes in a submarine canyon system (Polcevera and Bisagno canyons) in the Ligurian Sea (NW Mediterranean Sea), aiming at testing whether these large-scale incisions are peculiar systems, in comparison to the overlying water and the adjacent uncarved slope, in terms of biogeochemical and biological features. We analysed microbial communities' composition by high-throughput sequencing of 16S and 18S rRNA genes and their functional attributes by measuring heterotrophic carbon production, dissolved inorganic carbon fixation, respiration and the activity of the exoenzymes leucine aminopeptidase, alkaline phosphatase, beta-glucosidase and lipase. We found that both prokaryotic and eukaryotic communities were not significantly different inside the canyons (if compared to the close slope and overlying water), but they were rather shaped by the water masses dynamics in the area. The shallowest Modified Atlantic Waters, Levantine Intermediate Waters and Winter Intermediate Waters hosted higher percentages of Alphaproteobacteria, Bacteroidetes and Dinophyta, while the deepest Western Mediterranean Deep Waters hosted a higher fraction of Gammaproteobacteria, Chloroflexi, Discoba and Fungi. Among the functional measurements, only leucine aminopeptidase activity showed higher rates within the canyons. However, local hotspots within the canyons

Abbreviations: AMA, leucine aminopeptidase activity; AP, alkaline phosphatase activity; BGLU, beta-glucosidase activity; DIC, dissolved inorganic carbon; DICfd, dissolved inorganic carbon fixation rate: dissolved fraction; DICfp, dissolved inorganic carbon fixation rate: particulate fraction; DICftot, dissolved inorganic carbon fixation rate: total fraction; DOC, dissolved organic carbon; HCP, heterotrophic carbon production; LIP, lipase activity; LIW, Levantine Intermediate Water; MAW, Modified Atlantic Water; PCD, Prokaryotic Carbon Demand; PCoA, principal coordinate analysis; PN, Particulate Nitrogen; POC, particulate organic carbon; dbRDA, distance-based redundancy analysis; WIW, Winter Intermediate Water; WMDW, Western Mediterranean Deep Water

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characterised by high particulate matter loads and high C:N ratio (interpreted as refractory material from sediment local resuspension) displayed pronounced degradation activities.

1. Introduction

The dark portion of the Ocean (i.e. > 200 m depth) represents the largest biome on Earth, comprising about 75% of the whole volume of the planet's seas. Despite its importance, it still is the least explored set of ecosystems in the planet, mostly due to the challenges in accessing those habitats and the need for high-tech dedicated sampling instruments (Danovaro et al., 2014). In fact, only recently the efforts in studying the dark Ocean's ecological dynamics have been shedding lights on its biogeochemistry (Burd et al., 2010). Much attention has been directed toward understanding the unbalance between the amount of organic carbon reaching the deep sea through the sinking of particulate material from the surface ocean and the estimates of meso- and bathypelagic microbial activities, that could not be fuelled only by export (Burd et al., 2010). The discovery of pronounced bicarbonate fixation rates (e.g. Herndl et al., 2005; Celussi et al., 2017) and of slow sinking or buoyant organic particles (feeding heterotrophic metabolism; Baltar et al., 2009) are now at the base of researches on microbial dynamics in the deep water column. Although it could be regarded as a homogeneous environment, several features determine the dark ocean ecological inner variability. Among these, depth-related pressure gradients (Moesender et al., 2001; Celussi et al., 2009), water masses dynamics (i.e. oxygenation, advection and convection phenomena) (Hamilton et al., 2008; Celussi et al., 2010; Wilkins et al., 2013; Luna et al., 2016) and the variability in vertical fluxes of particulate organic carbon sinking to the bottom (Azam and Long, 2001) have the potential to structure microbial communities and their functioning.

The seafloor topography, which plays an important role in the ecology of deep-sea sediments (Zeppilli et al., 2016), could have an impact also on the overlying water column, especially in its deepest layers. For example, seamounts can alter local hydrological features, by conveying deep waters to shallower depths, potentially resulting in an upwelling of nutrients, or by modifying the fluxes of allochthonous material (retention mechanisms) (Clark et al., 2010 and references therein). Submarine canyons, incising the continental margins, generally act as major conduits of sediments and suspended material from shallow to deep-sea regions (Puig et al., 2014), although up-canyon transport is not uncommon (Amaro et al., 2016). A great variability characterizes the ecology of these structures. They are often regarded as biodiversity and biomass hotspots, fuelled by organic matter channelled from the shelf (Polymenakou et al., 2008; Fernandez-Arcaya et al., 2017) and promoted by their marked seafloor heterogeneity (Pierdomenico et al., 2017). However, the debate is still open and the knowledge on the 'canyon effect' on the overlying water column biota is even more limited. Canyons are prominent topographic features that modify the coastal circulation, and the intensification of both coast to ocean, and vertical water transport within submarine canyons is expected to affect the dynamics of plankton ecosystems in the vicinity of canyons (Guerreiro et al., 2014). In two independent modelling studies, Skliris and Djenidi (2006) and Muñoz et al. (2017) showed that the upwelling of deep water rich in nutrients, channelled into canyons in the NW Mediterranean, can enhance photosynthetic primary production at surface. Gili et al. (1999) reported three undescribed species of Hydroidomedusae in sediment traps placed in the Foix submarine canyon (Catalan coast), and hypothesised the presence of an unusually prolific plankton community in the canyon, probably supported by the continuous flux of organic matter from the continental shelf. Guerreiro et al. (2014) reported local hotspots of coccolithophore and phytoplankton biomass in the Nazarè canyon (central Portuguese margin), potentially associated with perturbations of surface water circulation by the canyon. Misic and Fabiano (2006), while examining a deep-canyon system in the Ligurian Sea, found that microbial communities inside these structures display enhanced organic matter degradation rates, as a consequence of irregular resuspension of organic and inorganic materials within the bottom sediments next to the canyon heads. However, the rapid and episodic flushing of canyons complicates the understanding of microbial communities' dynamics in their interior, and the question whether they can be considered as confined environments or fully embedded with the surrounding systems is still unanswered. This might depend on the morphological features of canyons, on the level of seawater mixing with upper-layers, and on their interplay with the local circulation system.

In the present study, we collected seawater samples from several stations located inside two submarine canyons in the Ligurian Sea (NW Mediterranean Sea), as well as in the adjacent continental slope. These canyons, Bisagno and Polcevera, are right-bounded canyons under the influence of the Northern Current (e.g., Barth et al., 2005). Due to the complex dynamics triggered by canyons (Spurgin and Allen, 2014) and episodic flushing by, e.g., turbidity currents (Puig et al., 2014), our hypothesis was that the Bisagno and the Polcevera canyons act as peculiar systems, with respect to the overlying water and the adjacent uncarved slope, in terms of biogeochemical and biological features. We tested the potential canyon effect on planktonic microbial features, by investigating microbial diversity (by high-throughput sequencing of 16S and 18S rRNA genes of prokaryote and protist communities, respectively) and activities (heterotrophic carbon production, dissolved inorganic carbon fixation, respiration and the microbial degradation potential of polysaccharides, lipids, polypeptides and phosphorylated organic compounds).

2. Methods

2.1. Study area

The Ligurian Sea is characterized by a general cyclonic circulation involving both the surface layer of Modified Atlantic Water (MAW) and the Levantine Intermediate Water (LIW) layer below (Barth et al., 2005). The system is generally described as oligotrophic. However, a permanent hydrological front leads to central upwelling and peripheral downwelling of water masses. In the former case, inorganic nutrients from LIW are provided to surface waters, stimulating primary production; in the latter, the freshly produced organic matter is allowed to sink, enriching the whole water column (Misic and Fabiano, 2006). Winter Intermediate Water (WIW) is a cooled and mixed MAW that reaches the buoyancy equilibrium between the MAW and the LIW layer, structuring into defined low-temperature thermohaline lenses (Gasparini et al., 1999). The bottom layer (> 1000 m) is generally occupied by Western Mediterranean Deep Water (WMDW), a dense water mass generated in the Gulf of Lions during winter (Testor et al., 2017).

The seafloor topography of the northern part of the Ligurian Sea presents a complex canyon system that incises the continental margin. Among the several canyons in the area, the Polcevera and the Bisagno (Fig. 1) are oriented in a NE-SW axis, present very steep slopes from the shelf break to about 1500 m and coalesce in the Genoa Valley at about 2000 m (Soulet et al., 2016).

2.2. Sampling and physico-chemical analyses

Fourteen stations in the Ligurian Sea (Fig. 1) were sampled between May 1st and May 6th 2013 (details on sampling stations are reported in