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Picoplankton distribution influenced by thermohaline circulation in the southern Adriatic

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A B S T R A C T

In this study, we focus on the interactive dynamics between physico-chemical processes and picoplankton distribution in order to advance our current understanding of the roles of various parameters in regulating picoplankton community structure in highly dynamic marine system such as the South Adriatic Sea. The research was carried out between October 2011 and September 2012 along the transect in the northern part of the South Adriatic Pit. The deep water convection occurred in the southern Adriatic during February 2012, with vertical mixing reaching the depth of 500 m. The picoplankton community was highly affected by this mixing event, whilst its compartments each responded differently. During deep water convection low nucleic acid heterotrophic bacteria (LNA HB) and *Synechococcus* had their lowest abundances (4×10^5 cell ml^{-1} and 8×10^2 cell ml^{-1}, respectively), picoeucaryotes had their highest abundances (10^4 cell ml^{-1}), while *Prochlorococcus* was absent from the area, most likely due to intense cooling and vertical mixing. In March 2012 Eastern Adriatic Current (EAC) brought warm and saline water with more nutrients, which resulted in the proliferation of high nucleic acid heterotrophic bacteria (HNA HB), having maximal abundance (4×10^5 cell ml^{-1}). The re-establishment of Levantine Intermediate Water (LIW) intrusion after the deep water convection resulted in the re-appearance of *Prochlorococcus* and maximal abundances of *Synechococcus* (4×10^4 cell ml^{-1}) in May 2012. The distribution of picoheterotrophs was mainly explained by the season, while the distribution of picophytoplankton was explained by the depth. Aside from nutrients, salinity was an important parameter, affecting particularly *Prochlorococcus*. The re-appearance of *Prochlorococcus* in the southern Adriatic during the period of LIW intrusion, together with their correlation with salinity, indicates their potential association with LIW. The relationship between *Prochloroccocus* distribution and physico-chemical environmental parameters provides an important insight into the ecological roles and niche preferences of this group.

1. Introduction

The dynamics of plankton communities are forced by the physical system in which they are embedded. Physical forcing events occur over a variety of time scales, and can cause changes in taxonomic structures, as well as in biogeochemical functions. This link between the physical environment and distribution of marine microbes was conceptualized by Margalef's phytoplankton mandala, which separates groups of phytoplankton based on turbulence and nutrient availability (Margalef, 1979). Margalef's conceptual model focused principally on large phytoplankton, however, there is growing evidence indicating that physical forces could explain patterns of picoplankton distribution as well (Bouman et al., 2011; Schmoker and Hernández-León, 2013; Sohm et al., 2016). Because of the picoplankton mobility' limitation and sinking rates imposed by their small sizes, distribution of these cells is primarily determined by passive lateral advection and vertical mixing in the water column. For these reasons, picoplankton is an ideal subject for investigating species patterns and their distribution in relation to the physical properties of the water column. Vertical mixing changes nutrient and light availability, and in doing so stimulates or disables growth of plankton communities. Within picophytoplankton, *Prochlorococcus* typically exists in stratified oligotrophic waters at temperatures above 17 °C, while *Synechococcus* and picoeukaryotes are characteristic for winter and early spring, when the water column is deeply mixed (Schmoker and Hernández-León, 2013). The water column mixing and low temperatures are considered as limiting factors

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for *Prochlorococcus* population (Bouman et al., 2011) due to their limited ability of chromatic adaptation (Bouman et al., 2006). On average, *Prochlorococcus* is restricted to warmer and oligotrophic oceans, while being absent in colder and nutrient-rich waters at high latitudes (Biller et al., 2005). *Prochlorococcus is* typically most abundant at or near the surface, while sharply decreasing below 150 m depth, likely being limited by light availability (Johnson et al., 2006). In comparison, *Synechococcus* does not extend as deep in the water column as *Prochlorococcus*, but it has a wider geographical distribution that covers both polar and high-nutrient waters (Flombaum et al., 2013). The Mediterranean Sea is in general dominated by *Prochlorococcus*, especially in the surface layer, up to 90 m (Moran et al., 2001; Jacquet et al., 2010) and its eastern part is considered as one of the most oligotrophic areas with *Prochlorococcus* abundances going up to 10^5 cell ml^{-1} (Mella-Flores et al., 2011). On the contrary, the western part of the Mediterranean Sea is more mesotrophic due to the influence of Atlantic waters and tends to be under the dominance of *Synechococcus* (Mella-Flores et al., 2011). In general, between these two cyanobacteria, there is an evident prevalence of *Synechococcus* in the Adriatic Sea (Radić et al., 2009; Šilović et al., 2012; Šantić et al., 2013), while *Prochlorococcus* is more prominent in the southern Adriatic than in its middle and/or northern part (Šilović et al., 2011; Babić et al., in press). These reports on southern Adriatic were case studies covering only the spring (May 2011; Šilović et al., 2011) and winter periods (end of February till the beginning of March 2015; Babić et al., in press) in the coastal and open southern Adriatic waters. Only one study covers *Prochlorococcus* dynamics in a whole year, however, restricted to coastal area (January to December 2005; Šantić et al., 2013). There is a general lack of knowledge on seasonal distribution of the complete picoplankton community (HNA and LNA HB, *Prochlorococcus, Synechococcus,* picoeucaryotes) in the southern Adriatic while in many studies covering phytoplankton, its smallest compartment (i.e. picoplankton) was often considered as one group (Batistić et al., 2012; Cerino et al., 2012; Lučić et al., 2017).

The interaction between the Mediterranean and its northernmost basin, the semi-enclosed Adriatic Sea, has an important influence on both physical and biological properties of both basins.

The Adriatic Sea acts as a dilution basin, exporting freshwater to the Ionian Sea while receiving saline and warmer water from it. The main inflow current characterising the Adriatic Sea is Eastern Adriatic Current (EAC) flowing from the Strait of Otranto along the eastern side (Orlić et al., 1992) (Fig. 1). On the other hand, Western Adriatic Current (WAC) can be observed in the surface and intermediate layers along the western Adriatic coast (Manca et al., 2001). The prevalent opinion is that EAC culminates in winter, but may peak in spring again (Orlić et al., 2006), bringing to the Adriatic Sea relatively warm, saline and oligotrophic Levantine Intermediate Water (LIW). LIW is a distinctive water mass originating in the eastern Mediterranean Sea, which usually occupies the intermediate layers (200–400 m) of the Mediterranean. It is formed in the Levantine basin (the eastern part of the Mediterranean) by the relatively deep vertical mixing in winter and preconditioned by increasing the salinity due to the evaporation in summer (Lascaratos et al., 1999). The first peak in EAC usually occurs in February and it is mostly related to coastal freshwater input and offshore evaporation, while the second one may appear in May due to wintertime surface cooling of the Adriatic when warmer conditions prevail over the Mediterranean (Orlić et al., 2006). The inflow of LIW through the northern Ionian Sea is regulated by the Adriatic-Ionian Bimodal Oscillating System (BiOS) mechanism (Gačić et al., 2010). BiOS is an internal mechanism which determines the upper-layer circulation (anticyclonic or cyclonic) in the northern Ionian Sea and hence is capable of shaping the thermohaline properties and the biogeochemical pool in the Southern Adriatic (Civitarese et al., 2010). During the cyclonic BiOS phase saline LIW enters the Adriatic, while during the anticyclonic BiOS regime the southern Adriatic is under the influence of less saline Atlantic Water (AW) from the western Mediterranean. Reversals of this northern Ionian circulation are occurring on a decadal time scale and are influencing the salt content of the adjacent basins, the Adriatic Sea, and the Levantine basin. The salt content in turn, influences the density of the intermediate and deep waters. The last cyclonic phase in the northern Ionian Sea started in the second half of 2011 (Mihanović et al., 2013; Gačić et al., 2014).

In January-February 2012 an intense cold outbreak occurred in the northern and middle Adriatic, and resulted in the formation of exceptionally dense waters (Mihanović et al., 2013). At the same time the deep water convection took place in the southern Adriatic (Bensi et al., 2013), with vertical mixing reaching the 500 m depth (Najdek et al., 2014). Such winter convection events are more likely to occur when the Ionian circulation is cyclonic and saltier waters of Levantine origin enter the southern Adriatic. By analysing salinity in the southern Adriatic, Ljubimir et al. (2017) noticed changes in year-to-year variability, which allowed them to distinguish 2011 as a less saline year (when anticyclonic circulation prevailed during most of the year) and 2012 as a more saline year (when cyclonic circulation prevailed). Moreover, Ljubimir et al. (2017) observed the shift in dominance of different groups of the phytoplankton community in cyclonic vs. anticyclonic years, and even disappearance of coccolitophorids during cyclonic BiOS phase. These findings emphasised the deep water

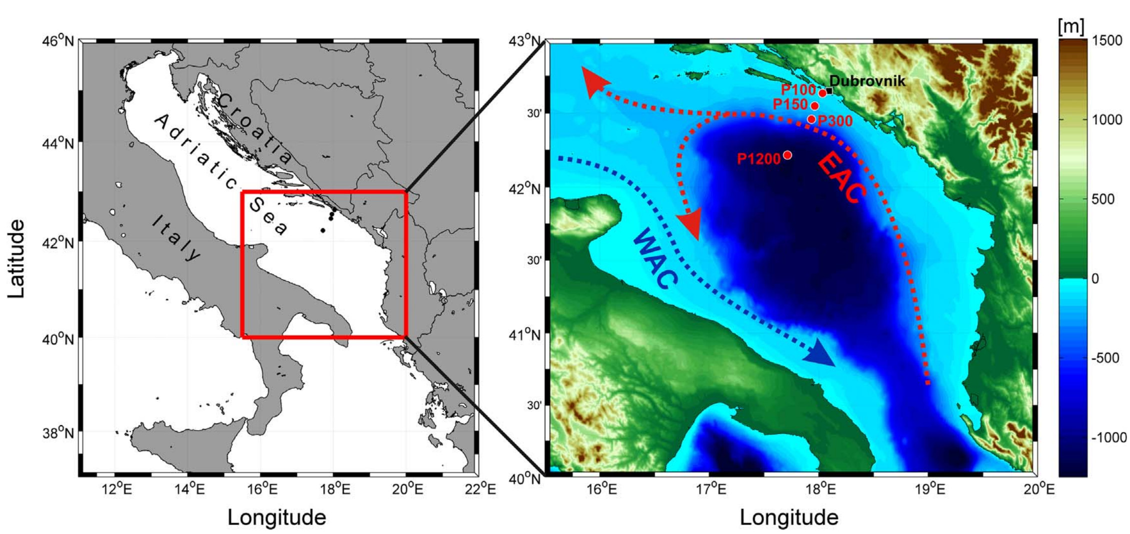

Fig. 1. Sampling stations in the southern Adriatic Sea. Major surface current systems are also indicated: Eastern Adriatic Current (EAC) and Western Adriatic Current (WAC).