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Sea surface temperature control of taxon specific phytoplankton production along an oligotrophic gradient in the Mediterranean Sea

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ABSTRACT

The current study aimed to assess changes in phytoplankton composition and productivity along an oligotrophic gradient in relation to changes in sea surface temperature (SST). Phytoplankton pigments, nutrients, and physical water column properties were studied along a longitudinal transect in the Mediterranean Sea (MED) in May–June 2013, covering its western (wMED) and eastern (eMED) basins. Pigments were used to determine phytoplankton taxonomic composition and taxon specific carbon fixation, whereas beam attenuation was used to calculate particulate organic carbon (POC). Nitrate, phosphate, and silicate concentrations integrated over 0–125 m declined from wMED to eMED (on average 13, 9, and 2 fold lower in eMED compared with wMED, respectively) and correlated inversely with SST (16.2–23.0 °C) for the whole transect in the Mediterranean Sea.
N:P ratios in the euphotic zone averaged 5.6 and 3.1 for wMED and eMED respectively, suggesting that phytoplankton was nitrate limited. Average phytoplankton productivity and biomass were 4 and 2.5 fold higher in the wMED than in the eMED, respectively. Relative abundances of diatoms, prasinophytes, dinoflagellates, and cryptophytes showed inverse correlations with SST and positive correlations with nutrient concentrations. In contrast, pelagophytes, chlorophytes, euglenophytes, *Synechoccocus* and *Prochlorococcus* showed positive correlations with SST and negative correlations with nutrient concentrations. Particulate organic carbon (POC) of the upper 200 m showed up to 3 fold higher concentrations in the wMED than in the eMED, and correlated positively with chlorophyll concentrations, productivity, and nutrient concentrations, and inversely with SST. Inverse correlations were observed for phytoplankton biomass and SST below 19 °C. SST above 19 °C as observed in the eMED did not correlate with phytoplankton biomass and productivity, showing that in this temperature range phytoplankton productivity is uncoupled from nutrient supply from deep water. This suggests different responses of Mediterranean phytoplankton to changes in SST, depending on the temperature range.

1. Introduction

Temperature records of the Mediterranean Sea (MED) have shown significant warming during the last decades (Malanotte-Rizzoli et al., 2014). The changes in sea water temperature occur both at the surface and at depth and are not uniformly distributed in the MED. Over the past 25 years, the eastern basins experienced a mean temperature increase of 0.77 °C, whereas the western basins warmed on average by 0.54 °C (Macias et al., 2013). This warming trend has been explained by variability in the Atlantic Multi decadal Oscillation (AMO) and by anthropogenic forcing (Macias et al., 2013). The warming trend in the MED and the oceans in general is expected to continue during this century (Levitus et al., 2000). This raises questions about the effect of ocean warming on marine productivity.

Typically, warming of the open ocean has been associated with an increase in the strength of stratification (Behrenfeld et al., 2006). This reduces exchange with nutrient rich deep waters and leads to nutrient limitation in the surface waters. In addition, warming may lengthen the period of stratification. Therefore, ocean warming is associated with a decline in phytoplankton productivity, and with changes in phytoplankton composition in temperate and warm temperate sections of the ocean (Behrenfeld et al., 2006; Polovina et al., 2008; Van de Poll et al., 2013). However, the coupling of phytoplankton productivity and abundance with stratification is less clear in oligotrophic oceanic regions (Chaves et al., 2010). Nevertheless, strong inverse correlations have been observed for sea surface temperature (SST) and remote sensing resolved chlorophyll a (chl-a) in the MED, both on seasonal and longer time scales (Volpe et al., 2012). This suggests that the mechanism described previously is indeed relevant for controlling Mediterranean phytoplankton productivity. Therefore, SST may be a useful proxy for

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phytoplankton productivity as it incorporates information on nutrient concentrations stratification strength, and the duration of stratification (Agawin et al., 2000; Van de Poll et al., 2013), and can be monitored by remote sensing.

Due to its semi enclosed status the Mediterranean Sea differs in many aspects from the neighboring open ocean. Low density, nutrient depleted Atlantic surface (~upper 200 m) waters enter the MED in the Alboran Sea and gradually mix with Mediterranean waters, resulting in increased surface density from west to east. At intermediate depth (200–600 m), a reverse flow of more saline water masses from the east Mediterranean Sea (eMED) exits via Gibraltar (Huertas et al., 2012). Therefore, in contrast to the open ocean, salinity increases with depth in the MED, thereby enhancing stratification. In addition to salinity, surface temperature increase from west to east. Overall the Mediterranean Sea has a negative nutrient budget, which is sensitive to river and atmospheric influx (Huertas et al., 2012).

Reported high N:P ratios in the eastern basin suggested phosphate limited productivity (Krom et al., 1991; Diaz et al., 2001) but this idea was recently challenged (Tanaka et al., 2011). In contrast, the western basins appear nitrate limited in spring but may develop phosphate limitation during summer (Marty et al., 2002). Related to the gradient is physical characteristics, the Mediterranean Sea is characterized by seasonal phytoplankton blooms in the western basins (Marty et al., 2002), whereas the eastern basins show less seasonal variability in phytoplankton production due to a deep nutricline for nitrate and phosphate (Vidussi et al., 2001). Productivity estimates are higher in the wMED than for the eMED (Uitz et al., 2012). Furthermore, the contribution of small phytoplankton species increases from west to east in the MED (Siokou-Frangou et al., 2010).

In the present study, we investigated the strength of the relationships of SST with nutrient concentrations and phytoplankton biomass, productivity, and taxonomic composition, and particulate organic carbon along a longitudinal transect in the Mediterranean Sea. The objective was to gain insight in the coupling of phytoplankton productivity, biomass, composition and SST, and the results are discussed in the context of the changes in temperature in the Mediterranean Sea.

2. Methods

Presented data were collected from 24 stations during a longitudinal cruise in the Mediterranean Sea onboard RV Pelagia (GEOTRACES Mediterranean cruise, 64PE370, May, June 2013). The cruise was executed in a west to east direction and included stations in the Alboran Sea, Algerian Basin, Sicily Channel, Ionian Sea and the Levantine Basin (Fig. 1). We defined the Sicily Channel as the transition from the west Mediterranean Sea (wMED: 10 stations) to the east Mediterranean Sea (eMED: 14 stations). Sampling was performed by a CTD rosette system with 24 large volume Niskin bottles (25 L), Seabird 9 + CTD, photosynthetically active radiation (PAR) (Satlantic), chlorophyll fluorescence (Chelsea Aquatracka) and beam attenuation (Wetlabs C-star) sensors. Phytoplankton and nutrients samples were taken in a dedicated container.

2.1. Physical parameters

SST was calculated as the average temperature in the upper 10 m. The depth of surface mixed layer was defined according to Levitus et al. (2000), as the depth where the temperature is 0.5 °C below SST. The strength of stratification was determined as the difference in potential density (sigma theta) between the surface and 200 m.

2.2. Nutrient concentrations

Nutrient samples (dissolved inorganic phosphate, nitrate, nitrite, and silicate) were filtered (0.2 μm Acrodisc) and measured onboard using a Bran and Luebbe Quaatro autoanalizer. Depth integrated phosphate, nitrate, and silicate concentrations (0–125 m) were generated by linear regression of nutrient concentration profiles in the upper 200 m (8–10 samples). Integration over the upper 125 m provides information of the proximity of the nutricline to the surface, and the 125 m depth interval also approximates the potential limit of the euphotic zone. N:P ratios were calculated as $(NO_x - NO_2) / PO_4$. N:P ratios were averaged for samples from above the DCM and for samples from the DCM to a depth of 150 m, as determined from chlorophyll-a (chl-a) fluorescence profiles. This distinction was introduced due to the varying responses of this parameter in the described depth interval.

2.3. Phytoplankton pigments

Seawater (5–10 L) from 4 depths (10–160 m) per station was filtered through GF/F (Whatman) using 0.3 mbar vacuum. Filters were snap frozen in liquid nitrogen and stored at −80 °C. For analysis, filters were freeze dried for 48 h and pigments were extracted using 90% acetone (v/v) for 48 h (4 °C, darkness). Pigments were separated by High Performance Liquid Chromatography (HPLC, Waters 2695) with a Zorbax Eclipse XDB-C8 column (3.5 μm particle size), using the method of Van Heukelem and Thomas (2001) modified after Perl (2009). Detection was based on retention time and diode array spectroscopy (Waters 996) at 436 nm. Pigments were manually quantified using standards (DHI lab products) except for divinyl chlorophyll b, which molar extinction coefficient was assumed identical to chl-b.

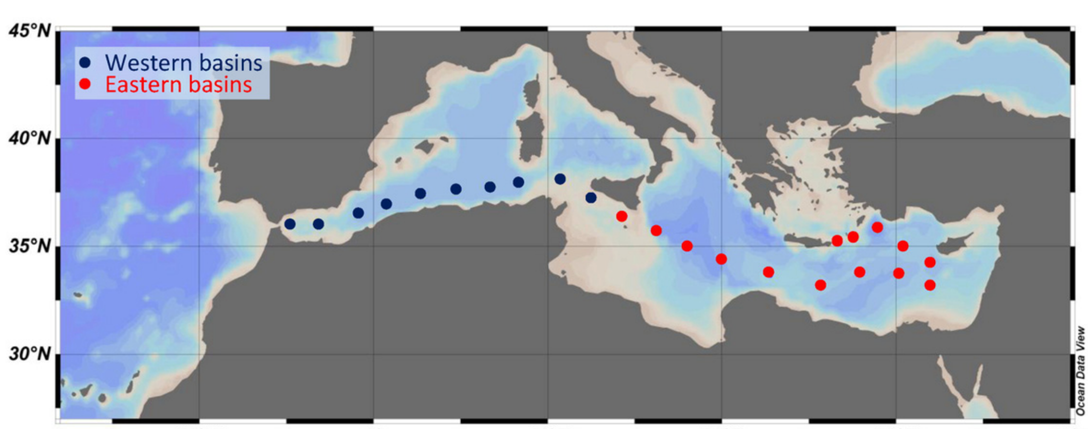

Fig. 1. Stations in the western and eastern basins during the GEOTRACES cruise (RV Pelagia 64PE370) in the Mediterranean Sea (May, June 2013).