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Particulate and dissolved primary production along a pronounced hydrographic and trophic gradient (Turkish Straits System–NE Aegean Sea)

A. Lagaria [a,b], S. Psarra [a,*], A. Gogou [c], S. Tuğrul [d], U. Christaki [b]

[a] Hellenic Centre for Marine Research, Institute of Oceanography, 71003 Heraklion, Crete, Greece
[b] Université du Littoral Côte d'Opale, ULCO, Laboratoire d'Océanologie et de Géosciences, LOG UMR CNRS 8187, 32 av. Foch, F-62930 Wimereux, France
[c] Hellenic Centre for Marine Research, Institute of Oceanography, 19013, Anavyssos, Greece
[d] Middle East Technical University, Institute of Marine Sciences, P.O Box 28, 33731, Erdemli-Mersin, Turkey

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ABSTRACT

The rates of particulate (PPp) and dissolved primary production (PPd) were estimated along a trajectory of variable environmental regimes formed in a narrow shelf area, following the course of Black Sea water masses (BSW) passing through the Turkish Straits System (TSS) into the NE Aegean Sea (BS–AS outflow). Seven stations in total were sampled, covering a transect from the eastern edge of the Marmara Sea basin to the NE Aegean Sea, during two consecutive cruises performed in October 2008 within the framework of the EU SESAME project. Along the BS–AS outflow, depth-integrated over the surface BSW layer PPp decreased considerably from 91 to <16 mg C m^{-2} h^{-1} whereas PPd increased from 3 to 10 mg C m^{-2} h^{-1}. As a consequence, the relative importance of PPd over total production (percentage extracellular release, PER) increased from 6% (±3% sd) in the Marmara Sea to 37% (±4% sd) in the NE Aegean Sea. Total chlorophyll *a* concentration gradually decreased and phytoplankton community size-structure was modified, with pico-phytoplankton, that originally represented 35% (±9% sd) in the Marmara Sea, gradually becoming dominant in the NE Aegean (77% ± 2% sd), substituting large nano- and micro-phytoplankton cells (>5 μm). This study showed that PER increased along a gradient from mesotrophy to oligotrophy, probably due to nutrient deficiency constraining phytoplankton growth and was closely related to phytoplankton size-structure. In the oligotrophic NE Aegean Sea, phytoplankton exudation was a significant source of dissolved organic carbon for heterotrophic prokaryotes.

1. Introduction

Studies over the last decades have suggested that dissolved organic carbon (DOC) photosynthetically produced and released by phytoplankton cells, i.e. dissolved primary production (PPd), accounts for a significant portion of total primary production (Baines and Pace, 1991; López-Sandoval et al., 2011; Thomas, 1971). They also suggest that it has a high ecological value, as it contributes to the pool of labile DOC fuelling heterotrophic prokaryotes with the necessary metabolic energy (Carlson, 2002; Cole et al., 1982; Williams, 2000). Therefore, PPd displays a functional role diverging from the classical one of primary production, where the organic carbon produced via photosynthesis and retained into the phytoplankton cells (particulate primary production) is channeled to higher trophic levels of marine planktonic food webs. There is an increasing need to explicitly record the spatial and temporal variability of dissolved primary production (PPd) and to comprehend its specific importance within the different marine environments. Moreover, there is a special interest for such studies in oligotrophic environments where interactions between phytoplankton and heterotrophic prokaryotes are complex, characterized both by competition for mineral nutrients and commensalism through DOC release from phytoplankton and uptake by heterotrophic prokaryotes (Bratbak and Thingstad, 1985; Joint et al., 2002).

In the Mediterranean Sea, along the established eastward increasing oligotrophy gradient of biomass and primary production (Ignatiades et al., 2009; Moutin and Raimbault, 2002; reviewed in Siokou-Frangou et al., 2010), the relative importance of PPd over total primary production, i.e. Percentage Extracellular Release (PER), was recently found to remain rather constant, with PER averaging approximately 37% within the basin (López-Sandoval et al., 2011). Other studies performed in various systems with different ecological characteristics, e.g., different hydrographic regimes and highly different trophic conditions and production levels between them, have shown that PER provides higher values in oligotrophic environments and decreases with increasing total production (Morán et al., 2002b; Teira et al., 2001a, 2003). It has been then suggested by López-Sandoval et al. (2011) that when variability of PPd is examined within the same system, PER tends to remain relatively constant over space and time (López-Sandoval et al., 2010; Marañón et al.,

* Corresponding author.
E-mail address: spsarra@hcmr.gr (S. Psarra).

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2004), but when contrasting environments are considered, the relative importance of PPd is considerably higher under oligotrophic conditions, as it has also been shown during inorganic nutrient additions experiments with surface Mediterranean waters (Lagaria et al., 2011).

PER is also found to be related to phytoplankton community size structure; for example, it has been observed that in environments where pico-phytoplankton and small nano-phytoplankton prevail, PER is relatively high, e.g. 42% (Teira et al., 2001a, 2001b). Theoretically, this may be attributed to the elevated surface/volume ratio of pico-phytoplankton, permitting important passive diffusion of small metabolites through the cell membrane (Bjørnsen, 1988; Kiørboe, 1993). Nevertheless, the relationship between PER and phytoplankton size-structure is not always evident (López-Sandoval et al., 2010, 2011).

The Turkish Straits System (TSS, including the Bosporus Straits, Marmara Sea and Dardanelles Straits), together with the NE Aegean area, which are naturally connected, form a "natural laboratory" with different water masses (Zervakis and Georgopoulos, 2002) and pronounced trophic (Beşiktepe et al., 1994) and production gradients (Frangoulis et al., 2010; Zervoudaki et al., 2011). The less saline, colder and lighter, mesotrophic Black Sea waters (BSW) are exported to the upper layer of the Marmara Sea basin and finally reach the saline, denser oligotrophic waters of the Aegean Sea. In the opposite way, the dense Mediterranean waters of Levantine origin (Levantine Water, LW) enter the Marmara Sea basin through the Dardanelles Straits and sink to a depth corresponding to its modified density, as a function of seasonal input flux variations and interior stratification (Beşiktepe et al., 1994). As a result, driven by the density difference between the Black Sea and the Aegean Sea waters, the Marmara Sea presents a two-layer stratification system with a strong water circulation in the upper layer directed towards the Aegean Sea (Polat and Tuğrul, 1996; Stanev and Peneva, 2002). Along the way, the properties of the surface Black Sea water progressively change through encounter and diffusive mixing with the deeper layers of Levantine origin; referred to as modified Black Sea Water (MBSW). Moreover, phytoplankton biomass, abundance and production present apparent decreasing trends from the Marmara Sea to the NE Aegean Sea (Zervoudaki et al., 2011).

In the present study we measured the particulate and dissolved primary production along this narrow shelf area characterized by a pronounced gradient of trophic conditions, following the outflow of the Black Sea water masses through the TSS to the NE Aegean Sea. Based on the findings of previous studies (López-Sandoval et al., 2011; Morán et al., 2002a, 2002b) our hypothesis was that phytoplankton exudation would vary importantly along these environmental attributes. Furthermore, we tested whether PER variability was related to phytoplankton size-structure and the extent at which dissolved primary production may supply the carbon requirements of heterotrophic prokaryotes under oligotrophic conditions, in the NE Aegean Sea.

2. Methods

2.1. Study site and sampling

Samples were collected during two consecutive oceanographic cruises undertaken within the EU-SESAME IP project; the first cruise was performed in the Marmara Sea and the Dardanelles Straits (1-5/10/2008) on board the Turkish R/V BILIM, and the second was performed in the NE Aegean Sea (9-11/10/2008) on board the Greek R/V AEGAEO. In total, seven shelf stations were sampled, covering a transect from the edge of the Marmara Sea to the NE Aegean Sea (Fig. 1). All stations were visited in the morning (usually between 09:00 and 10:00 local time), except for St. 6 that was visited in the afternoon (13:00–14:00 local time). A suite of biogeochemical parameters (mineral nutrients, total and size-fractionated chlorophyll *a*, particulate and dissolved primary production, size-fractionated primary production) was assessed with *in situ* sampling within the euphotic zone of the water column. The depth of 1% surface irradiance in the NE Aegean Sea reaches the 80–100 m depth (Ignatiades et al., 2002), whereas in the Marmara Sea the light penetration hardly exceeds the upper BSW layer (<30 m, Ediger and Yilmaz, 1996). Consequently, in the Marmara Sea sampling was performed at four standard depths of the surface layer (1–2 m, 10 m, 20 m, 30 m), while along the shelf of the NE Aegean Sea area, two additional standard depths (50 m, 65–75 m) were sampled. Bacterial production was measured only at the NE Aegean Sea stations (St. 5, 6 and 7, Fig. 1).

2.2. Hydrography

Vertical profiles (0–80 m) of temperature, salinity and fluorescence were obtained by the Sea-bird Electronics CTD System (911 plus and SBE-25 during the first and second cruises, respectively), and the different water masses (BSW, MBSW, LW) were identified at each station. Transparency of the waters was assessed by means of the Secchi disc depth measured before noon. The incident light was measured in the NE Aegean Sea by a JYP1000 optical sensor attached on board, mounted on a freely illuminated spot.

2.3. Inorganic nutrients

For the determination of inorganic nutrients concentrations, triplicate seawater samples were filtered through membrane filters (0.45 μm pore size) and collected in 100 ml polyethylene bottles. Determination of phosphate concentration was performed on-board according to Murphy and Riley (1962), while samples for determination of nitrate + nitrite were kept frozen (−20 °C) until analysis in the laboratory, according to Strickland and Parsons (1977).

2.4. Chlorophyll a

The amount of chlorophyll *a* (chl*a*) was measured fluorometrically, according to Yentsch and Menzel (1963). In order to assess the amount of total chl*a*, 200–300 ml (in the Marmara Sea) or 1 l (in the NE Aegean Sea) of seawater were filtered through polycarbonate 0.2 μm filters (47 mm), while additional 1 l seawater samples were filtered through 2.0 μm (47 mm) and 5.0 μm (47 mm) polycarbonate filters, in order to assess the quantity that corresponded to the 0.2–2.0 μm, 2.0–5.0 μm and >5.0 μm fractions, respectively. Filters were kept frozen in the dark until extraction in 90% acetone solution overnight, and the measurements were performed with a TURNER 112 fluorometer. Phytoplankton community size-structure was determined by the estimation of the three fractions mentioned above, assuming that they corresponded to pico-phytoplankton (p-PHY: 0.2–2.0 μm), small nano-phytoplankton (n-PHY: 2.0–5.0 μm) and larger nano- and micro-phytoplankton (nμ-PHY: >5.0 μm).

2.5. Particulate and dissolved primary production

Particulate and dissolved primary production rates were assessed according to the ^{14}C incorporation method (Steemann-Nielsen, 1952), as modified by Marañón et al. (2004) for the dissolved primary production measurements. For each sampling depth, three light and one dark polycarbonate 170-ml bottles were filled with the seawater sample, each one spiked with 20 μCi of $NaH^{14}CO_3$ tracer and incubated for approximately 2 h *in situ*. This was generally done around midday, when the incident irradiance was at its greatest thus yielding maximum primary production rates, except from St .6 where incubation took place later during the day. At the end of the incubation, two 5-ml aliquots were taken from each bottle, filtered through 0.2 μm filters (25 mm) and the filtrate was collected for determination of the dissolved primary production. The remaining 160-ml was filtered through 0.2 μm (47 mm) filters and the filter was collected for determination of the