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

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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.,

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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

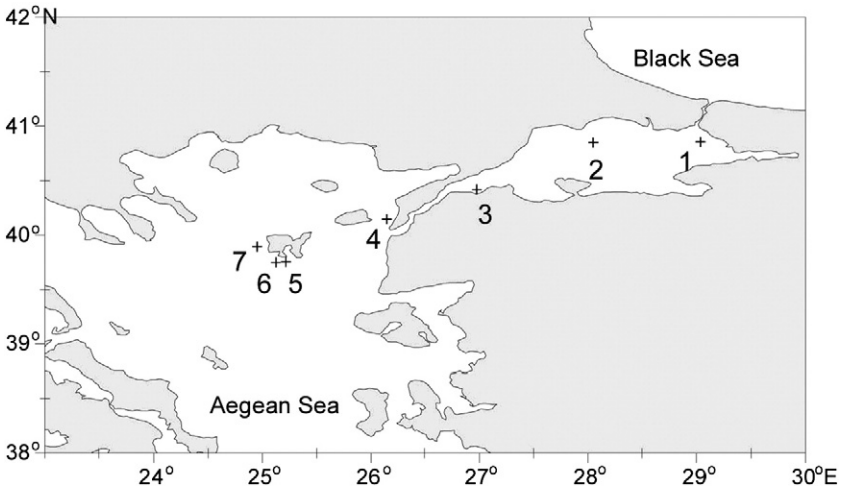

Fig. 1. Location of stations sampled during the SESAME-II cruises in October 2008.

particulate primary production rate. Additionally, in order to assess the particulate primary production that corresponded to the different size fractions of phytoplankton community, two additional 320-ml water samples were collected from each depth and filtered through 2.0 μm and 5.0 μm filters (47 mm). All filtrations were performed under low vacuum pressure (50–150 mmHg). To remove excess ^{14}C-bicarbonate, filters were soaked in 1 ml 0.1 N HCl and left in open polyethylene 5-ml vials overnight, while filtrates collected in 20-ml scintillation vials were acidified with 100 μl of 50% HCl and left open overnight in an orbital shaker. After the addition of 4 ml and 10 ml of scintillation cocktail for filters and filtrate, respectively, the radioactivity was measured in a scintillation counter. PPp and PPd rates were calculated by subtracting the counts per minute of the dark bottles (cpm_{dark}) from the respective light ones (cpm_{light}). We used a value of 27,600 mg C m^{-3} for the concentration of dissolved inorganic carbon (DIC, Triantaphyllou et al., 2010) and a value of 1.05 for the isotopic discrimination factor. The formula used for the calculation of PPp and PPd was:

$$\mathrm{PPp, PPd}\left(\mathrm{mg\ C\ m^{-3}h^{-1}}\right)=(\mathrm{incubated\ volume/filtered\ volume})\times\left[\left(\mathrm{cpm_{light}}-\mathrm{cpm_{dark}}\right)\times \mathrm{DIC}\times 1.05\right]/(\mathrm{cpm_{total}}\times \mathrm{h}), \quad (1)$$

where cpm_{total} were the counts per minute of the total amount of tracer inoculums and h the duration of the incubation.

Particulate primary production rates of the 0.2–2.0 μm, 2.0–5.0 μm and >5.0 μm fractions that corresponded to p-PHY, n-PHY and nμ-PHY, respectively, were then assessed by subtraction of the respective filters. Total primary production, i.e. the sum of PPp and PPd, was considered as a close approximation of the gross primary production (GPP) assuming that the short-time incubations minimised any significant respiratory losses. Net daily PPp rate was calculated from the hourly rates according to the model proposed by Moutin et al. (1999), and daily PPd rate was calculated considering a constant DOC-release rate during (1) the light period only (PPd_{light}) and (2) over 24 h (PPd_{24h}).

2.6. Bacterial production and carbon demand

Bacterial production (BP, *sensus stricto* referring to all-heterotrophic prokaryotes' production, *Eubacteria* and *Archaea*) was measured at the standard depths in the NE Aegean Sea (St. 5, 6, and 7) using the ^{3}H leucine incorporation technique (Kirchman, 1993) coupled to the centrifugation method (Smith and Azam, 1992). For water samples at each depth, duplicate aliquots (1.5 ml) inoculated with 22 nM of leucine (a mixture of 8 nM of ^{3}H-leucine and 14 nM of 'cold' leucine) and a TCA-killed control were incubated for 2 h at *in situ* temperature in the dark. The ^{3}H-leucine incorporation rate into TCA-insoluble fraction was converted into carbon units using 1.5 kg C per mol leucine incorporated (Kirchman, 1993).

Bacterial carbon demand was estimated as the sum of bacterial production and respiration, with the latter obtained from the empirical model of Robinson (2008) that derives bacterial respiration from BP. Estimated BCD was converted to daily rates by multiplying by 24.

2.7. Depth-integrations

Integrations of biological parameters were obtained following the trapezoid rule. Euphotic-zone depth differs by >2-fold among the sampled sites (see Section 2.1), thus a variable integration depth was applied (over the 0–30 m, 0–65 m and 0–75 m layers in the Marmara Sea, the Dardanelles Straits and the NE Aegean Sea, respectively). In order to follow modifications of production and community structure within the BSW–MBSW upper layer depth-integrated values of primary production rates were also presented for the upper 0–30 m layer for all stations.

3. Results

3.1. Hydrography and inorganic nutrients

The vertical profiles of temperature and salinity revealed that in the Marmara Sea (St. 1, 2 and 3) the water column was characterized by two distinct layers with fairly different temperature and salinity levels: the upper BSW (salinity <25 psu) and the deeper LW (salinity = 38.7 psu), separated by a steep halocline located between 15 and 25 m (Fig. 2). The station located in the Dardanelles exit (St. 4), displayed a surface mixed layer of MBSW within the 0–20 m layer and the halocline occupied a wide intermediate layer between 20 and 55 m, to be followed by a deeper LW layer (Fig. 2) down to the bottom (73 m, Table 1). In the NE Aegean Sea (St. 5, 6 and 7) the water column was characterized by a thin MBSW surface layer (uppermost 10 m) of low salinity (36.5 psu) and a wide halocline located between 10 and 35 m, while below was the denser and more saline (>39 psu) LW (Fig. 2). Overall, salinity of the upper BSW–MBSW layer (<30 m, Fig. 2) presented a clear increasing trend, from <25 psu to ~36.5 psu, along the Black Sea–Aegean Sea (BS–AS) outflow of the water masses and could therefore be used as a gradient descriptor.

Along the Black Sea–Aegean Sea (BS–AS) outflow, the transparency of the waters, as shown by the Secchi disc readings, increased from 5 m at St. 1 to 20 m at St. 7 and the average per station concentrations

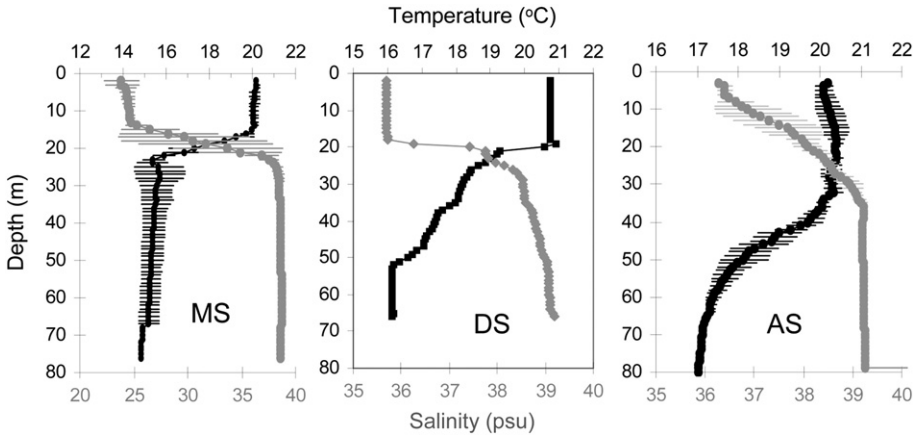

Fig. 2. Temperature and salinity profiles of the stations located in the Marmara Sea (MS), the Dardanelles Straits (DS), and the Aegean Sea (AS).

of $NO_3 + NO_2$ and PO_4 in upper BSW–MBSW layer decreased (Table 1), showing 16- to 30-fold higher values in the Marmara Sea.

3.2. Chlorophyll a and phytoplankton size-structure

The chlorophyll maximum, as determined by *in situ* fluorescence profiles obtained by CTD readings, was located in the upper BSW layer (<20 m) in the Marmara Sea while it was located within the LW (>50 m) in the Dardanelles and NE Aegean Sea (Table 1). For uniformity, the term "deep chlorophyll maximum" – DCM for chlorophyll maximum was used at all stations, including those with shallow depth maxima as in the Marmara Sea. Overall, total chl*a* values presented a wide range from <0.1 μg L^{-1} in the NE Aegean Sea to 2.1 μg L^{-1} in the Marmara Sea (Fig. 3). p-PHY was the main fraction determining the vertical structure of the phytoplankton community in the NE Aegean Sea (St. 1–3) and the Dardanelles Straits (St. 4, Fig. 3), while the larger nμ-PHY cells specified the vertical profiles of chl*a* in the Marmara Sea. Small nano-phytoplankton (2.0–5.0 μm) displayed no perceptible vertical patterns, with the exception of St. 2 in the Marmara Sea where it peaked at 20 m (Fig. 3).

Depth-integrated chl*a* in the upper BSW–MBSW layer (0–30 m) decreased from 37 to 3 mg m^{-2} along the BS–AS outflow and the phytoplankton community size structure was gradually modified (Fig. 4). nμ-PHY prevailed (51% ± 1% of total chl*a*) in the Marmara Sea, while in the NE Aegean Sea p-PHY dominated (77% ± 2%). n-PHY was generally <20% of total chl*a* at all stations. When considering a larger layer of the water column (0–75 m) in order to also include the DCM in the NE Aegean Sea, integrated chl*a* of the three phytoplankton size-fractions showed similar patterns to the 0–30 m integrations; total chl*a* decreased from 37 to <13 mg m^{-2} (Fig. 4).

3.3. Particulate and dissolved primary production rates

PPp rates generally decreased from the Marmara Sea towards the NE Aegean Sea, as also indicated by its negative correlation with salinity ($r = -0.766$, $p < 0.001$, $n = 36$) while PPd rates did not show any relative significant trend ($p = 0.12$).

PPp rates presented a range of values from <0.2 mg C m^{-3} h^{-1} in the Aegean Sea to >4.0 mg C m^{-3} h^{-1} in the Marmara Sea). PPp displayed maxima in the uppermost 5 m-layer at all stations, except at St. 4 located in the Dardanelles exit where PPp presented the highest rate at 30 m depth (Fig. 5). PPp rates decreased rapidly below 20 m depth in the Marmara Sea, while in the NE Aegean Sea the decrease with depth was gradual (Fig. 5).

PPd rates were less variable than PPp and did not present a constant pattern with depth. PPd overall ranged from 0.04 to 0.46 mg C m^{-3} h^{-1}, and represented 1.3% to 81% of GPP (Fig. 5).

It should be noted that exceptionally St. 6 presented 2 to 3-fold lower PPp rates than the nearby Aegean stations, St. 5 and 7, as it was sampled after noon and thus measured rates did not correspond to the max hourly rates; nevertheless, PPd rates presented similar values at all three NE Aegean stations (Fig. 5). As a result, the vertical profile of PER at St. 6 presented higher values, e.g. >40% at all depths, than St. 5 and 7.

Depth-integrated rates in the upper BSW–MBSW layer (0–30 m) are presented in Table 2. Max hourly PPp (excluding St. 6 which was sampled in the afternoon, see Sections 2.1 and 2.5 in methods) ranged from 8.9 to 91.5 mg C m^{-2} h^{-1} presenting a clear decreasing trend along the BS–AS outflow, while PPd showed an opposite pattern, increasing along the BS–AS outflow from 3.3 to 10.9 mg C m^{-2} h^{-1} (Table 2). The resultant PER increased from 4% in the Marmara Sea to 40% in the NE Aegean Sea, and reached an even higher value (61%) in the afternoon sampled St. 6 (Table 2). The corresponding estimated net PPp daily rates (see Section 2.5) ranged from 32.6 to 349.5 mg C m^{-2} d^{-1}, presenting the highest values in the Marmara Sea, while the daily PPd rates calculated for a constant DOC release rate during the light period only (PPd_{ligth}) and for a 24 h period (PPd_{24h}), ranged from 37.4 to 121.9 mg C m^{-2} d^{-1} and 80 to 261 mg C m^{-2} d^{-1}, respectively, presenting the highest values in the NE Aegean Sea (Table 2).

Table 1
Area, location and physico-chemical parameters (mean and range of the upper 0–30 m layer) of the seven sampled stations. DCM: Deep chlorophyll maximum depth as determined by fluorescence CTD readings, $NO_3 + NO_2$: nitrate + nitrite, PO_4: phosphate.

Station	Area	Latitude	Longitude	Bottom depth (m)	Secchi disc depth (m)	DCM (m)	$NO_3 + NO_2$ (μM)	PO_4 (μM)
1	Marmara	40 51.687 N	29 2.259 E	86	5	17	3.82 (0.16–10.41)	0.48 (0.02–1.04)
2	Marmara	40 51.258 N	28 2.943E	1226	7	20	2.42 (0.07–5.42)	0.10 (0.02–0.27)
3	Marmara	40 25.305 N	26 58.561E	71	9.5	7	1.78 (0.08–4.48)	0.17 (0.02–0.32)
4	Dardanelles	40 8.860 N	26 8.812E	73	17	52	0.07 (0.06–0.08)	0.03 (0.02–0.03)
5	NE Aegean	39 45.171 N	25 12.97 E	96	15	60	0.08 (0.05–0.14)	<0.02
6	NE Aegean	39 44.945 N	25 7.478E	107	10	60	0.06 (0.05–0.08)	<0.02
7	NE Aegean	39 53.651 N	24 57.108E	117	20	60	0.14 (0.08–0.28)	<0.02

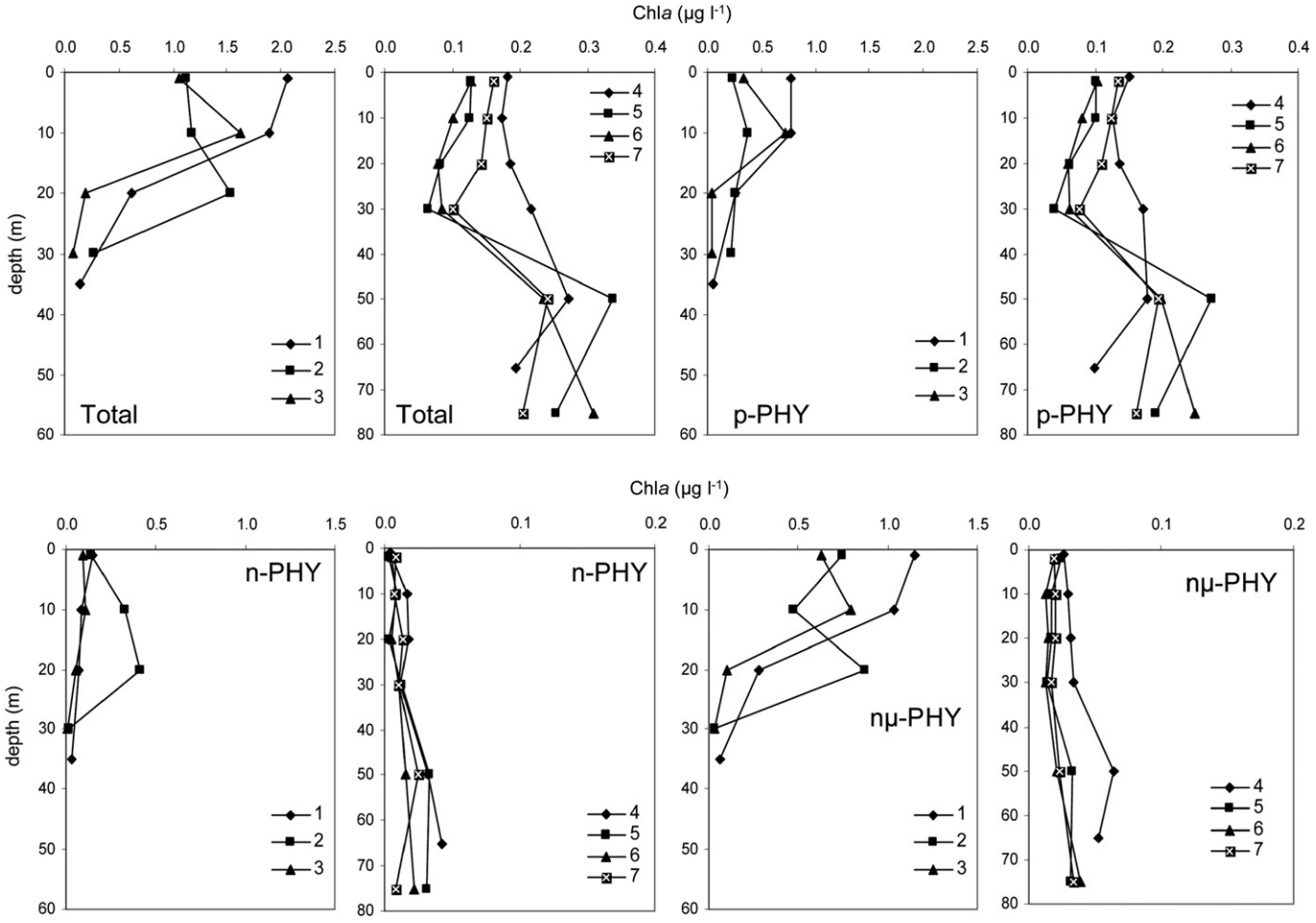

Fig. 3. Vertical distribution of total and size fractionated chlorophyll *a* (p-PHY: 0.2–2.0 µm, n-PHY: 2.0–5.0 µm, nµ-PHY: >5.0 µm) in the Marmara Sea (St.1–3), and the Dardanelles Straits and NE Aegean Sea (St. 4–7).

p-PHY was responsible for 40–44% and 62–78% of the hourly PPp rates in the Marmara and Aegean Sea, respectively (Table 2). nµ-PHY contributed >40% to PPp in the Marmara Sea, with exception of St. 2 where it contributed 18%, and 21–29% to PPp in the NE Aegean Sea (Table 2).

When considering the entire euphotic zone of the areas (0–30 m in the Marmara Sea, 0–75 m in the Aegean Sea, see Section 2.7), integrated PPp ranged from 16.0 to 91.7 mg C m^{-2} h^{-1} presenting the highest values in the Marmara Sea, and PPd ranged from 4.4 to 25.7 mg C m^{-2} h^{-1} presenting the highest values in the NE Aegean Sea. The corresponding PER, estimated by euphotic-depth integrated PPp and PPd, was 5–11% in the Marmara Sea, 32% in the Dardanelles Straits and 44–46% in the NE Aegean Sea.

Pooling data from all stations, no significant relationship was found between PPd and PPp ($p = 0.80$) or total chl*a* ($p = 0.27$). PPd was moderately correlated with PPp ($r^2 = 0.56$, $p = 0.04$) and total chl*a* ($r^2 = 0.55$, $p = 0.04$) only within the Marmara Sea (St. 1, 2 and 3).

3.4. PER and phytoplankton size-structure

In order to relate the dynamics of PPd to the phytoplankton size-structure, PER values, obtained by volumetric PPp and PPd

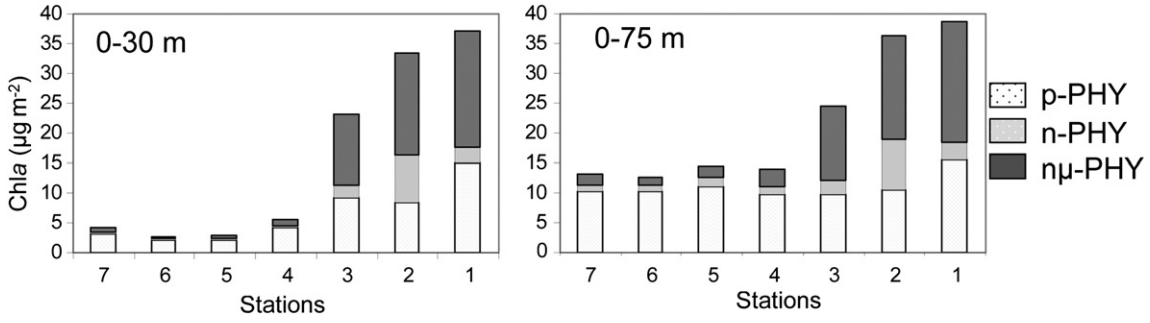

Fig. 4. Integrated chl*a* of the difference size fractions (p-PHY: 0.2–2.0 µm, n-PHY: 2.0–5.0 µm, nµ-PHY: >5.0 µm) over the 0–30 m and 0–75 m layer.

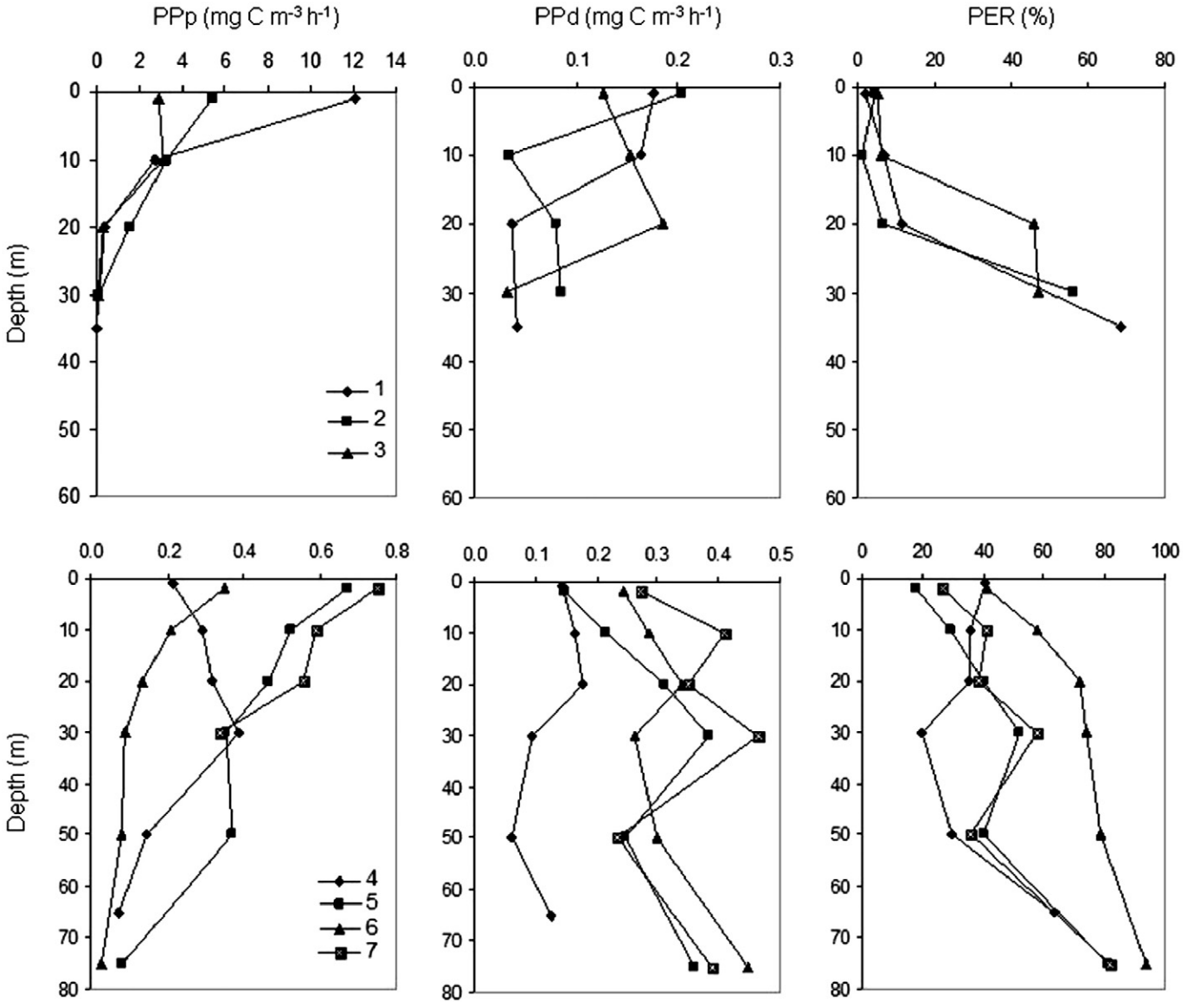

Fig. 5. Vertical profiles of particulate (PPp), dissolved primary production (PPd) and percentage extracellular release (PER) in the Marmara Sea (St. 1–3, upper panels) and the Dardanelles Straits and NE Aegean Sea (St. 4–7, lower panels).

rates, were plotted against the chl*a* percentage contribution of p-PHY and nμ-PHY (Fig. 6). A significant positive exponential relationship was obtained between PER and p-PHY (Fig. 6a) and a negative one was obtained between PER and nμ-PHY (Fig. 6b). p-PHY and nμ-PHY contributions to chl*a* explained 39% and 50% of the variability in PER ($p < 0.001$), respectively (Fig. 6).

3.5. Heterotrophic prokaryotes in relation to primary production in the NE Aegean Sea

In the NE Aegean Sea (St. 5, 6 and 7), BP ranged from 7.3 to 16.9 μg C m^{-3} h^{-1}. It displayed maximum values at the uppermost 10 m layer and gradually decreased with depth (Fig. 7), following the

Table 2
Depth-integrated primary production rates over the surface BSW–MBSW layer (0–30 m). PPp: Particulate primary production, p-PHY and nμ-PHY PPp: contribution of pico-phytoplankton and large (>5 μm) phytoplankton cells to PPp, respectively, PPd: dissolved primary production, PER: Percentage extracellular release, PPd_{light}, PPd_{24h}: daily dissolved primary production rates (see Section 2.5).

Station	PPp (mg C m^{-3} h^{-1})	p-PHY PPp (%)	nμ-PHY PPp (%)	PPd (mg C m^{-3} h^{-1})	PER (%)	PPp (mg C m^{-3} d^{-1})	PPd_{light} (mg C m^{-3} d^{-1})	PPd_{24h} (mg C m^{-3} d^{-1})
1	91.5	42	57	4.2	4	349.5	46.9	100.4
2	73.5	44	18	3.3	4	312.5	37.4	80.0
3	46.7	40	44	5.3	10	178.9	59.6	127.6
4	8.9	–	–	4.5	34	31.6	50.9	108.9
5	14.5	65	20	7.6	34	59.6	86.5	185.2
6	5.4	62	29	8.5	61	32.6	95.3	204.1
7	16.3	78	21	10.9	40	57.1	121.9	261.0

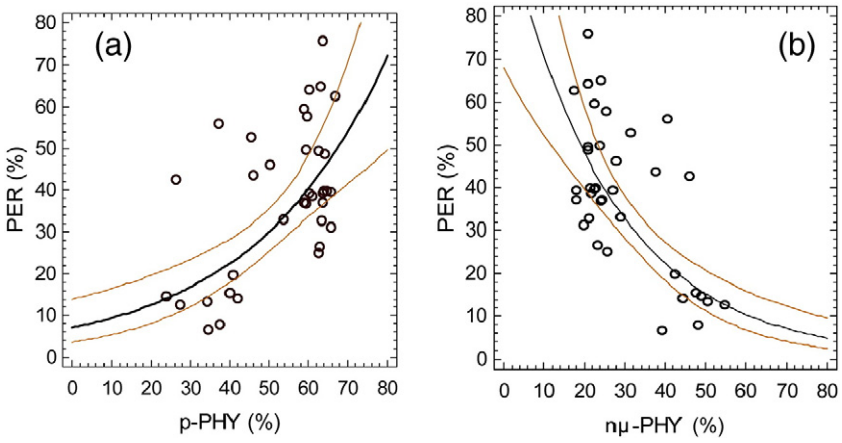

Fig. 6. Relationship between PER and percentages of a) p-PHY chl*a*: $PER = 7.03e^{0.02(\%p - PHY)}$, $r^2 = 0.39$, $p < 0.001$, $n = 36$, b) nμ-PHY chl*a*: $PER = -103.4e^{0.04(\%n\mu - PHY)}$, $r^2 = 0.50$, $p < 0.001$, $n = 36$.

same pattern with PPp with which it was positively correlated ($r^2 = 0.56$, $p = 0.02$).

Euphotic-zone-integrated (0–75 m) BCD (see Section 2.6) ranged 16.6–18.0 mg C m^{-2} h^{-1} and represented on average 50% (±11% sd) of GPP and 74% (±8% sd) of PPd (Table 3). When comparing the estimated daily rates (see Sections 2.5 and 2.6), integrated BCD represented 119% (±20% sd) or 64% (±9%) of the daily total primary production (Table 3), depending on the way that the daily PPd rates were estimated: calculated for a constant DOC release rate during the light period only (PPd_{ligth}) or for a 24 h period (PPd_{24h}), respectively.

When examining the entire volumetric dataset in the NE Aegean Sea we did not find a statistically significant log–log linear relationship between volumetric BCD and GPP hourly rates ($p = 0.08$, Fig. 8a). However, when excluding the afternoon sampled St. 6 we obtained a significant relationship (Fig. 8b, $p < 0.001$).

4. Discussion

The spatial variability of particulate and dissolved primary production was recorded along a pronounced gradient of hydrographic and trophic regimes formed in a narrow shelf area, following the outflow of the Black Sea water masses through the Turkish Straits System (TSS) to the Aegean Sea (BS–AS outflow).

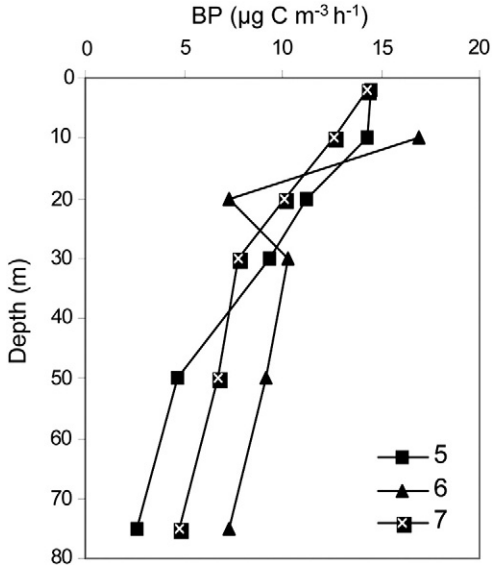

Fig. 7. Vertical profile of bacterial production (BP) in the NE Aegean Sea (St. 5, 6 and 7).

The several-fold decreasing trends of all chemical and phytoplankton-related parameters recorded, such as inorganic nutrients, chlorophyll *a*, particulate primary production and the modification of phytoplankton size-structure, in parallel with the change of water masses properties as specifically indicated by salinity, revealed a gradual shift from rather mesotrophic conditions in the Marmara Sea, where nano- and micro-phytoplankton dominated, to oligotrophic ones in the NE Aegean, with the prevalence of pico-phytoplankton. Some interesting observations were obtained from comparison of these finding with the respective biological measurements in the same area during the preceding spring time (April 2008, Zervoudaki et al., 2011). It seems that there wasn't any pronounced variability between the two seasons studied within the TSS area since both chl*a* and PP values were in the same levels, while pico-phytoplankton contribution to chl*a* was slightly higher during April. However, in the oligotrophic NE Aegean area, primary production presented ~ a 2-fold decrease in the fall.

An interesting finding in our study was that the longitudinal distribution of dissolved primary production did not follow the decreasing trends of the other phytoplankton-related parameters along the BS–AS outflow, presenting, on average, 2-fold higher integrated values over the upper BSW–MBSW layer in the NE Aegean Sea than in the Marmara Sea. The contrasting patterns of the depth-integrated PPd and PPp resulted in highly important changes in the percent extracellular release (PER), which increased progressively along the BS–AS outflow (Table 2) and was on average 6% (±3% sd) and 37% (±4% sd) in the BSW–MBSW layer in the Marmara Sea and the NE Aegean Sea, respectively. The recorded range of PER values is in accordance with values reported in similar comparative studies, where PER was <10% under productive and 30–42% under oligotrophic conditions (Morán and Estrada, 2001; Teira et al., 2001a, 2001b). Also, PER corresponding to the whole euphotic layer in the NE Aegean Sea (44–46%) was close to values reported in east Mediterranean open waters (33–42%, López-Sandoval et al., 2011).

The observed variations of PER along the BS–AS outflow could be partly attributed to variations in the phytoplankton size structure, as shown by the close relationship of PER with the phytoplankton size classes (Fig. 6). PER presented the highest values when pico-phytoplankton was dominant (>55%), while it decreased to <20% when the larger than >5.0 μm nano and micro-phytoplankton where prevailing (>45%). This may be assumed to be an indication of the 'passive diffusion' mechanism, i.e. diffusion of low molecular weight metabolites through the cell membrane, which is, theoretically, expected to be more efficient when small cells dominate due to their elevated surface/volume ratio (Bjørnsen, 1988). It should be noted however, that the amount of chl*a* corresponding to pico-phytoplankton did not vary significantly among the stations (Kruskal–Wallis test, $p = 0.07$). The highly marked differences in the relative contribution of the different size-groups to total

Table 3
Depth-integrated (0–75 m layer) bacterial production (BP) and estimated bacterial carbon demand (BCD), and ratios of hourly BCD with gross (GPP) and dissolved primary production (PPd) and of daily BCD with daily total primary production (PP_{total}) in the NE Aegean Sea (St. 5–7).

Station	BP (mg C m^{-2} h^{-1})	BCD (mg C m^{-2} h^{-1})	BCD:GPP	BCD:PPd	BCD:PP_{total} (PPp + PPd_{ligth})	BCD:PP_{total} (PPp + PPd_{24})
			Hourly rates	Hourly rates	Daily rates	Daily rates
5	0.59	16.6	0.41	0.65	0.98	0.54
6	0.68	18.0	0.62	0.77	1.39	0.71
7	0.61	17.3	0.46	0.81	1.21	0.67
Avg ± sd			0.50 ± 0.10	0.74 ± 0.08	1.19 ± 0.20	0.64 ± 0.09

chl*a* were due to the significant decrease (Kruskal–Wallis, $p < 0.001$) of the amount of chlorophyll *a* corresponding to large nano- and micro-phytoplankton along the BS–AS outflow. Consequently, if passive diffusion was the dominant mechanism, phytoplankton exudation would have been a fairly constant process, even if its relative contribution to total primary production differed among the stations. In this study, however, 1.8-fold on average higher volumetric exudation rates were observed in the NE Aegean Sea (Fig. 5), indicating that most probably there is an additional mechanism responsible for exudation.

According to 'overflow mechanism', i.e. active release of excess photosynthate organic compounds by phytoplankton, exudation would be enhanced under high irradiances and nutrient-limited conditions (Fogg, 1983), which are usually found in surface oligotrophic waters. In a study with diatom's batch culture, it was shown that PER was higher when cells were growing under phosphorus-limited conditions of skewed N:P ratios compared to N-limited or N:P balanced conditions (Obernosterer and Herndl, 1995), and in a nutrient-additions experiment with natural populations it was shown that PER was higher when either N or P was deficient than when both nutrients were in excess and presented a relatively balanced N:P ratio (Lagaria et al., 2011). Consequently, this confirms that nutrient availability has a key role to the release of dissolved organic matter by phytoplankton, since depletion of mineral nutrients constraints cell macromolecular synthesis inducing the active release excess photosynthetic compounds. In our study, the average mineral nutrient concentrations of the upper BSW–MBSW layer decreased progressively along the BS–AS outflow, resulting in quite depleted waters in both nitrite-nitrate and phosphate when finally reaching the NE Aegean Sea (Table 1). Consequently, these nutrient-depleted conditions might have caused the relative higher exudation rates in the NE Aegean Sea (Lagaria et al., 2011; López-Sandoval et al., 2011; Obernosterer and Herndl, 1995).

Trophic processes might have contributed as well to DOC release from phytoplankton cells (Carlson, 2002). When measuring PPd with the ^{14}C-incorporation method, there is no definitive way to distinguish labile compounds produced by physiological processes or trophic ones, such as e.g. grazing and/or cell lysis (Karl et al., 1989). However, the short-time incubations (2 h) performed in our study should have minimized any grazing impact on PPd measurements.

It is well known that the predominant factors regulating primary production rates are light and inorganic nutrients (De Baar, 1994; Kirk, 1994). Therefore, due to less light available for photosynthesis during the late incubation at St. 6 (mean incident light 585 ± 284 μmol photons m^{-2} s^{-1}), PPp rates were considerably lower than the ones recorded in the stations nearby (St. 5 and 7), where incubation for primary production experiments took place around midday (mean incident light 1399 ± 130 μmol photons m^{-2} s^{-1}) and thus yielded maximum rates. Nevertheless, light seemed to have a much lower effect on PPd than on PPp. Interestingly, PPd rates were similar at all NE Aegean stations, including the afternoon sampled St.6, indicating that diurnal light variations do not significantly affect phytoplankton exudation. This was in accordance with irradiance-production experiments where it has been shown that phytoplankton exudation does not present any variability with increasing irradiance (Marañón et al., 2005; Morán and Estrada, 2001), or that it presented much smaller variability than PPp across large irradiance gradients (0–2000 μmol photons m^{-2} s^{-1}), presenting higher PPd rates under irradiances below the saturation level (Marañón et al., 2004). The observation that diurnal variability does not significantly affect PPd is useful for converting hourly PPd rates to daily ones, since it confirms the hypothesis that DOC release from phytoplankton cells continues at a constant rate, at least during the daylight period.

The different extent at which light affects PPp and PPd can also explain, in part, the vertical profiles of production rates and PER. In the Marmara Sea the two-layer stratification system observed (Beşiktepe et al., 1994) results in concentrating autotrophic organisms and regeneration of particulate organic matter within the upper layer (Ergin et al., 1993; Polat et al., 1998) and limiting light penetration below the upper BSW layer (15–25 m, Ediger and Yilmaz, 1996). Consequently, primary production was restricted within the upper 0–20 m presenting maxima at the surface (1 m, Fig. 5). In the NE Aegean Sea, the much wider euphotic layer (Table 1) resulted in a smooth, gradual decrease of PPp with depth.

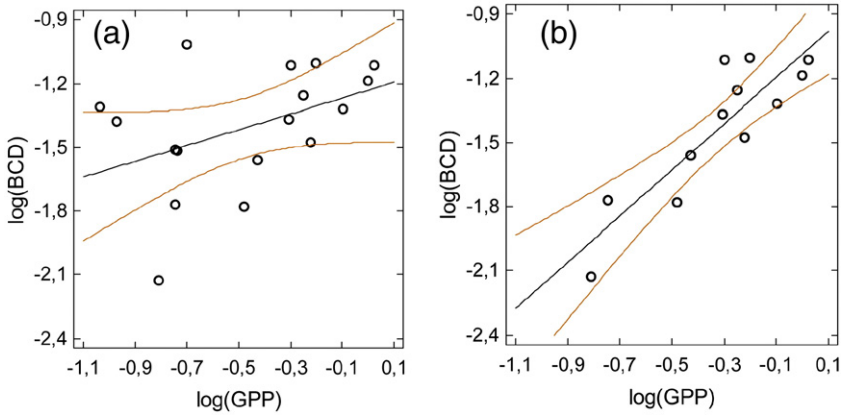

Fig. 8. Linear regression (Model II) of log-transformed gross primary production (GPP, mg C m^{-3} h^{-1}) and bacterial carbon demand (BCD, mg C m^{-3} h^{-1}) a) for the whole NE Aegean dataset (St. 5, 6 and 7): log (BCD) = 0.37 * log(GPP) − 1.23, $r^2 = 0.18$, $p = 0.08$ and b) for St. 5 and 7 only: log(BCD) = 1.08 * log(GPP) − 1.09, $r^2 = 0.77$, $p < 0.001$.

Contrary to PPp vertical profiles, PPd did not show a consistent pattern with depth (Fig. 5). As a result, the vertical distribution of PER displayed minimum values that coincided with PPp maxima, and relatively high values (>40–50%) at greater depths, where PPp was reduced. Although this has previously been observed (Marañón et al., 2004, 2005; Teira et al., 2001b), in other studies PER has generally been found to present variable patterns with depth (López-Sandoval et al., 2011; Teira et al., 2003).

In the NE Aegean Sea, the vertical BP profiles with maximum values at surface are typical for the area. However, recorded rates were lower than those reported previously for the same season (1.5–120 ng C l^{-1} h^{-1} in the 0–100 m in September, Christaki et al., 2003). Usually, in the NE Aegean Sea, BP rates are elevated compared to other Aegean Sea regions and this has been attributed to the influence of the BSW–MBSW mass (Christaki et al., 2003; Sempéré et al., 2002) that is enriched in dissolved organic carbon and dissolved organic nitrogen (Meador et al., 2010; Sempéré et al., 2002), rather than inorganic nutrients (Polat and Tuğrul, 1996). Based on BP production rates measured during our study, the estimated bacterial respiration according to the model of Robinson (2008) corresponded to a bacterial growth efficiency (BGE) of 3–4%, which falls within the range of BGE values reported in the NW Mediterranean coastal and offshore waters (2–8%, Gasol et al., 1998; Sempéré et al., 2003). Low BGE values imply slow growth of heterotrophic prokaryotes with investment in maintenance costs rather than in growth, which is proposed to be an adaptation mechanism in oligotrophic environments (del Giorgio and Cole, 1998).

In the literature, there is no definite and consistent way to demonstrate the dependence of heterotrophic prokaryotes on phytoplankton production and exudation, usually termed “coupling”. Previous studies have usually used correlations between bacterial and primary production rates (e.g. Cole et al., 1988; Conan et al., 1999; Turley et al., 2000) and comparisons of bacterial carbon demand (BCD) with PPp and PPd (e.g. Teira et al., 2001a, 2003; Van Wambeke et al., 2008). In our study, as far as hourly rates are concerned, BP was positively correlated to PPp, while a significant linear relationship was found between BCD and GPP (Fig. 8b). Moreover, both the GPP and the PPd exceeded the estimated BCD by 50% and 25%, respectively (Table 3), indicating that they should fulfill the carbon requirements of heterotrophic prokaryotes.

It may be argued, however, that comparison of hourly rates is not entirely reliable, since BCD and GPP evolve differently during the day. We therefore estimated and compared the daily rates of BCD, PPp and PPd, as well. The model used to calculate the daily PPp rates provides net rates, thus excluding both autotrophic respiration and exudation (Moutin et al., 1999). In order to calculate the daily PPd, we hypothesized that DOC release was constant during the day, which, as mentioned above, has been also confirmed in our study. Moreover, if phytoplankton extracellular release depends exclusively on photosynthetic rate, then DOC release (PPd_{ligth}) would cease in the dark (Marañón et al., 2004). In this case, the estimated daily BCD was balanced with the sum of the net PPp and PPd_{light} (Table 3), assuming that the daily GPP (including also autotrophic respiration) would even exceed BCD. Nevertheless, given that in natural environments phytoplankton cells encounter stress factors and are under grazing pressure, it would be expected that DOC release over a period of a day would be a joint effect of physiological and trophic processes (Karl et al., 1989). In this case, we may assume that DOC released continued also in the dark (PPd_{24}), which resulted in total production (the sum of net PPp and PPd_{24}) enough to fulfill the carbon requirements of heterotrophic prokaryotes (Table 3).

In conclusion, it has been shown that PER was higher under oligotrophic conditions, most probably due to nutrient limitation. Moreover, PER was related to phytoplankton size-structure, exhibiting higher values as the biomass of large cells decreased and pico-phytoplankton biomass became dominant. Also, diurnal light variations did not seem to directly control phytoplankton exudation. Moreover, all the different methods used for the estimation of BCD and of daily production rates, and the variable assumptions applied in each case, indicate that phytoplankton and heterotrophic prokaryotes in the NE Aegean Sea were closely coupled and that phytoplankton exudation was a significant source of DOC for heterotrophic prokaryotes, in this area and season. It is clear that the TSS-NE Aegean system is a unique natural laboratory for biological processes studies. Future work integrating seasonal variability of particular hydrographic features in relation to their trophic status will help to cover the seasonal range of processes and relationships presented in this work, and incorporate these results into predictive models of system budgets and functioning.

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