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Seasonal and spatial variation of bacterial production and abundance in the northern Levantine Sea

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Abstract

Spatial and temporal heterogeneity in bacterial production and abundance in relation to ambient bio-physicochemical parameters has been investigated in the Levantine Sea. Five stations with different trophic states in an area extending from highly eutrophic Mersin bay to the mesotrophic Rhodes gyre area including the oligotrophic offshore waters were sampled four times. Integrated bacterial production varied between 6.1 and 90.3 $\mu\text{g C m}^{-2} \text{d}^{-1}$ with higher rates occurring during September 2012 in offshore waters. Bacterial abundance ranged between 0.18 and 7.3×10^5 cells ml^{-1} within the euphotic zone and was generally higher up to 100 meters throughout the study period. In offshore waters, bacterial production (0.401 to 0.050 $\mu\text{g C m}^{-3} \text{d}^{-1}$), abundance (4.5 to 1.6×10^5 cells ml^{-1}) and depth of the productive layer decreased from 150 to 75 meters westward along the transect. Although the highest abundance was observed in July 2012 in offshore waters, the highest activity was measured in September 2012. These results indicated that the temperature played a key role in regulating bacterial abundance and production in the area. High chlorophyll concentrations in March did not correspond to high bacterial abundance and production at the same time. Increase in dissolved organic carbon content following spring phytoplankton bloom and the increase in temperature in the mean time might have enhanced the bacterial activity towards summer.

Keywords: Bacterial production, Heterotrophic bacteria, Rhodes Gyre, Cilician basin, Levantine Sea.

Introduction

Bacteria play a major role in the marine food web by acting efficiently on cycling of elements, degradation of organic matter and recycling of nutrients. They thrive in diverse ecological conditions in the seas and freshwater territories and consume 10 to 50% of carbon fixed by phytoplankton in the oceans (Azam *et al.*, 1983). The eastern Mediterranean is known as one of the ultra-oligotrophic basins among the world seas (Krom *et al.*, 1991; Ediger *et al.*, 2005; Psarra *et al.*, 2005; Yucel, 2008). Despite its highly oligotrophic nature of the eastern Mediterranean Sea especially in the offshore, shelf waters eutrophied due to anthropogenic sources (mainly transported by rivers) do exist in its northeastern sector along the Turkish coast. Besides some smaller rivers the perennial rivers Göksu, Lamas, Tarsus, Seyhan, Ceyhan and Asi account for a total fresh water flux much greater than the present discharge of the Nile in the eastern Mediterranean (Pinaridi *et al.*, 2006; Koçak *et al.* 2010). Oligotrophic offshore waters mingled with eutrophic shelf waters are transported westward via meandering Asia Minor current along the Anatolian coast (Özsoy *et al.*, 1989; 1991; 1993; Yucel, 2008). Also, Levantine Deep Water (LDW) originated from Atlantic Water pumps nutrient to euphotic zone while rising up in the Levantine Basin as an internal nutrient source

(Yılmaz & Tuğrul, 1998). The impacts of seasonal to inter-annual scale variations in the local circulation and mixing characteristics caused in changes in the production and transport of the water masses in the basin (Sur *et al.* 1993; Özsoy *et al.*, 1993; Malanotte-Rizzoli *et al.*, 1999). Also, nutrient-rich deep waters are carried to the euphotic zone in cyclonic Rhodes Gyre by the upwelling events, which further stimulate primary productivity in its periphery (Ediger *et al.*, 2005).

Microbial biomass is dominated by heterotrophic microorganisms in upper euphotic zone in the oligotrophic eastern Mediterranean (Tanaka *et al.*, 2007). The rate of bacterial production was found to be higher in the western part of the Mediterranean parallel to primary production, however bacterial abundances were surprisingly found very similar throughout the Mediterranean. Likewise, primary production and bacterial production showed similarities in western and eastern part of the Mediterranean Sea. This results suggest that primary production is an important organic carbon source for bacteria (Siokou-Frangou *et al.*, 2010 and references therein). Bacterial production is not only limited by phosphorus in the eastern Mediterranean, but also nitrogen and carbon limitation or co-limitation occurring in various depths (Siokou-Frangou *et al.*, 2010; Yucel, 2013). In addition, temperature has also been

suggested to be an important limiting factor on bacteria due to its influence on all chemical and biochemical processes (Pomeroy & Wiebe, 2001; Adams *et al.*, 2010; Gertman *et al.*, 2013). The substrate affinity of bacteria can also be affected by the temperature, for example bacteria can lose substrate affinity in colder temperature (Adams *et al.*, 2010).

The amount of data regarding bacterial activity in the study area (Mersin Bay) is very little (Zoppini *et al.*, 2010; Yucel, 2013). Previous studies generally focused on the western Mediterranean and the southern part of the Levantine Basin, which are well studied and understood (Siokou-Frangou *et al.*, 2010; Raveh *et al.*, 2015). Furthermore there are no data relating to the area in between the Cilician Basin and Rhodes Gyre.

The main objectives of this study based on the quantification of the *in-situ* bacterial production were to describe the spatio-temporal heterogeneity in bacterial production and abundance in the study area, and to identify effective factors. The results are a first contribution from a region characterized by a substantial lack of data, and thus provide background information for future studies in the northern Levantine Sea.

Methods

Sample collection and methodology

Samples for this study were collected from five stations in the northern Levantine Basin (Fig. 1, Table 1). Four cruises were undertaken in July and September 2012 and March and May 2013 on board of the R/V *Bilim-2* of the Institute of Marine Sciences, Middle East Technical University. Water samples from surface (0.5 m) and various depths up to 200 meters were collected using 5 liters capacity Nansen closing bottles attached to a rosette sampler housing a Sea-bird Electronics-911 plus CTD probe. In addition to *in-situ* bacterial production, bacterial abundance and chlorophyll *a* (Chl-*a*) together with associated physico-chemical variables (nitrate+nitrite, phosphate, temperature and salinity) were studied at all stations. CTD data were processed utilizing the standard Sea-Bird data processing software.

Nutrients

Nutrient (nitrite+nitrate and phosphate) samples from the bottle casts were stored and kept frozen in plastic bottles. Samples were analyzed by using a two-channel

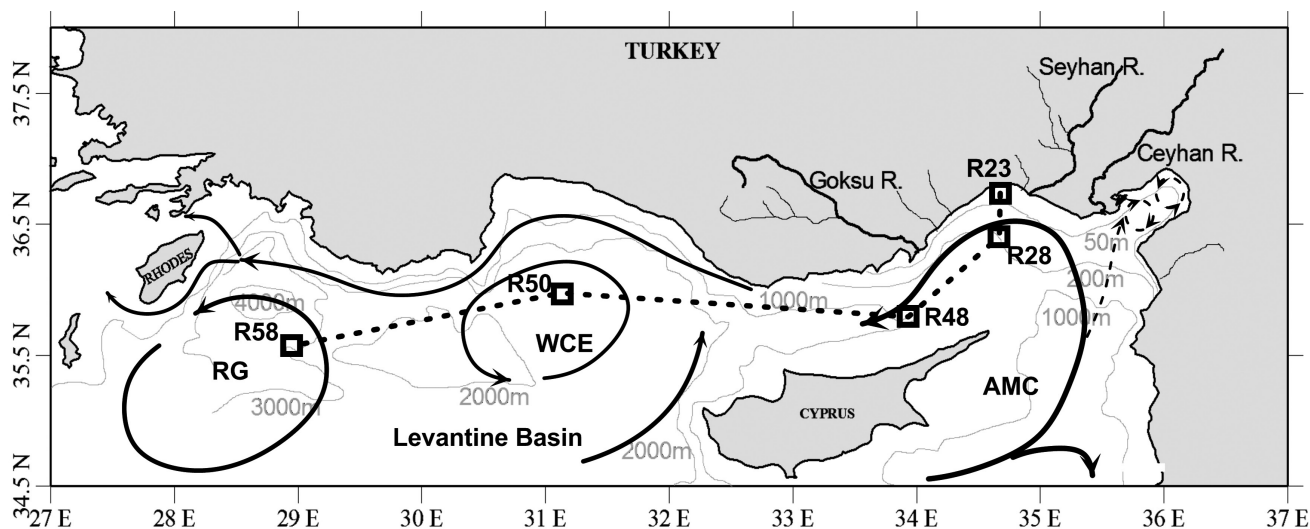


Fig. 1: Location of sampling stations in Levantine Basin including rivers, bathymetry and main currents (AMC-Asia Minor Current, WCE-West Cyprus Eddy, RG-Rhodes Gyre-modified from Siokou-Frangou *et al.*, 2010).

Table 1. List of sampling stations.

Stations	Position	Sampling Depth (m)	Depth (m)	Sampling Date
R23	36.700 °N, 34.700 °E	39	40	July 3-8, 2012
R28	36.300 °N, 34.700 °E	200	223	September 20-25, 2012
R48	35.871 °N, 33.981 °E	200	1006	
R50	35.750 °N, 31.000 °E	200	2320	March 12-21, 2013
R58	35.500 °N, 29.000 °E	200	2800	May 6-12, 2013

auto-analyzer (Technicon) according to Grasshoff *et al.* (1983). Detection limits for nitrate+nitrite and phosphate were 0.05 and 0.02 μM , respectively.

Chlorophyll *a*

Seawater samples (1-3 liters) were collected at selected depths for fluorometric assessment of Chl- *a* content. Samples were filtered through 47 mm GF/F filters at low vacuum. The filtrates were kept frozen at - 20°C. The filters were then extracted with 5 ml 90% acetone solution by using an ultrasonicator (60 Hz for 1 minute) and the volume of the extract was adjusted to 10 ml. The extracts were kept in the dark overnight (about 12 hours) at + 4 °C, then centrifuged at 3500 rpm for 10 minutes to remove the cellular debris. Fluorometric analysis was carried out by using a Hitachi F-2500 type fluorescence spectrophotometer. Chl-*a* concentration was calculated according to the formula given by Strickland & Parsons (1972).

Bacterial Abundance

For the enumeration of bacteria, 50 ml seawater transferred to dark borosilicate bottles were fixed with glutaraldehyde (0.625% final concentration). Samples were then stored at room temperature in the dark. 15 ml seawater from each sample was filtered onto black polycarbonate filter (0.2 μm pore-diameter, 25 mm diameter). During the filtration, 200 μl of acridine orange were added to the filtration funnel for staining (Hobbie *et al.*, 1977). Heterotrophic bacteria were enumerated by using an epifluorescence microscope (EFD3, Nikon). A minimum of 30 microscope fields were chosen at random and cells were counted on each slide. Cell counts were then transformed to cell numbers per milliliter.

Bacterial Production

Bacterial production was determined by the incorporation of ^3H -leucine by bacteria. Micro-centrifugation method was applied for extraction of ^3H -leucine (Smith & Azam, 1992). Sea water samples of 1.7 ml volume from selected depths were transferred to 2 ml centrifuge vials (three replicates and one blank). The bacteria in the blank vials were killed by the addition of 90 μl 100 % trichloroacetic acid (TCA). 10 μl of ^3H -leucine (specific activity 40-60 Ci mmol^{-1}) were added (final activity was 10 nM). Samples were incubated *in situ* for three hours at the selected depth. To kill bacteria after the incubation 90 μl 100 % TCA were added into all vials. Extraction was done in laboratory according to Smith & Azam (1992). Radioactivity was determined by using Perkin Elmer Tri-Carb 2810 TR Scintillation Counter. Leucine incorporation rate in bacterial production was converted to carbon by using leucine conversion factor (Kirchman, 1993). Depth dependent production rates are calculated by the trapezoidal method. Daily rates were calculated by multiplying hourly rates by 24.

Statistical methods

Principal Component Analysis (PCA) was used to summarize environmental variable inter-correlations and potential underlying environmental factor patterns/ gradients. Since skewness and the magnitude of the variables influence the resulting PCs, it is good practice to apply skewness transformation, center and scale the variables prior to the application of PCA. In order to optimize PCA analysis, we log- transformed the continuous variables as suggested by Venebles & Brian (2013). The hierarchical Ward's method based on minimum variance was used to perform the cluster analysis. All basic statistic and multivariate analysis were carried out using R software version 3.2.0 (R Core Team, 2014) with “*caret*” and “*ade4*” packages (Dray & Dufour, 2007; Kuhn, 2008).

Results

Temperature and Salinity

Water column temperature in the study area varied between 14.26 and 29.15 °C during the sampling period (Table 2). Thermocline was observed at ≈ 10 meters in May, and went deeper (20-60 m) and with well stratified waters in September 2012 in offshore stations (Fig. 2). Depth-dependent temperature decrease in offshore stations (R23-R58) was observed in all cruises except in March 2013, when temperature was distributed homogeneously along the entire water column, varying between 14.88 and 17.65°C among the stations. Meanwhile, except for May 2013 stratification was not observed at st. R23 in coastal waters, where water column was well mixed and with a homogeneous temperature profile but strong seasonal variations (Fig. 2).

Salinity ranged between 37.95 and 39.59 (Fig. 2, Table 2). The lowest salinity value (37.95) was observed at 3 m in the shelf station R23. Shelf waters of Mersin Bay are highly affected by increased freshwater fluxes especially during winter and spring from perennial rivers and little brooks. As a result, low salinity water mass at top 5 m is observed at station R23 during March and May. Atlantic Water ($S \leq 38.87$, 45-70 m) was detected in September 2012 in offshore stations (R28-R58) (Fig. 2). This layer was moving up towards west in the study area.

Nutrients

Nitrate+nitrite concentrations varying between 0.05 to 5.51 μM throughout increased with depth in offshore waters below the euphotic zone the study period. Highly reduced concentrations were typical of top 50 meters ($< 0.5 \mu\text{M}$). Higher concentrations were met at the cyclonic Rhodes Gyre area (St. R58) below 50 m, with a nutricline at around 75 m (Fig. 3). Presumably due to inputs from rivers, elevated concentrations were observed

in March 2013 at station R23. Compared to nitrate+nitrite, phosphate was independent of geographical location and depth. In general, phosphate levels were near to the detection limits (0.02 μM) in top 20 meters. Higher

concentrations were measured at station R50 and R58 below 50 meters. The highest concentration of 0.17 μM was recorded at 200 m at the cyclonic Rhodes Gyre station R58 during summer.

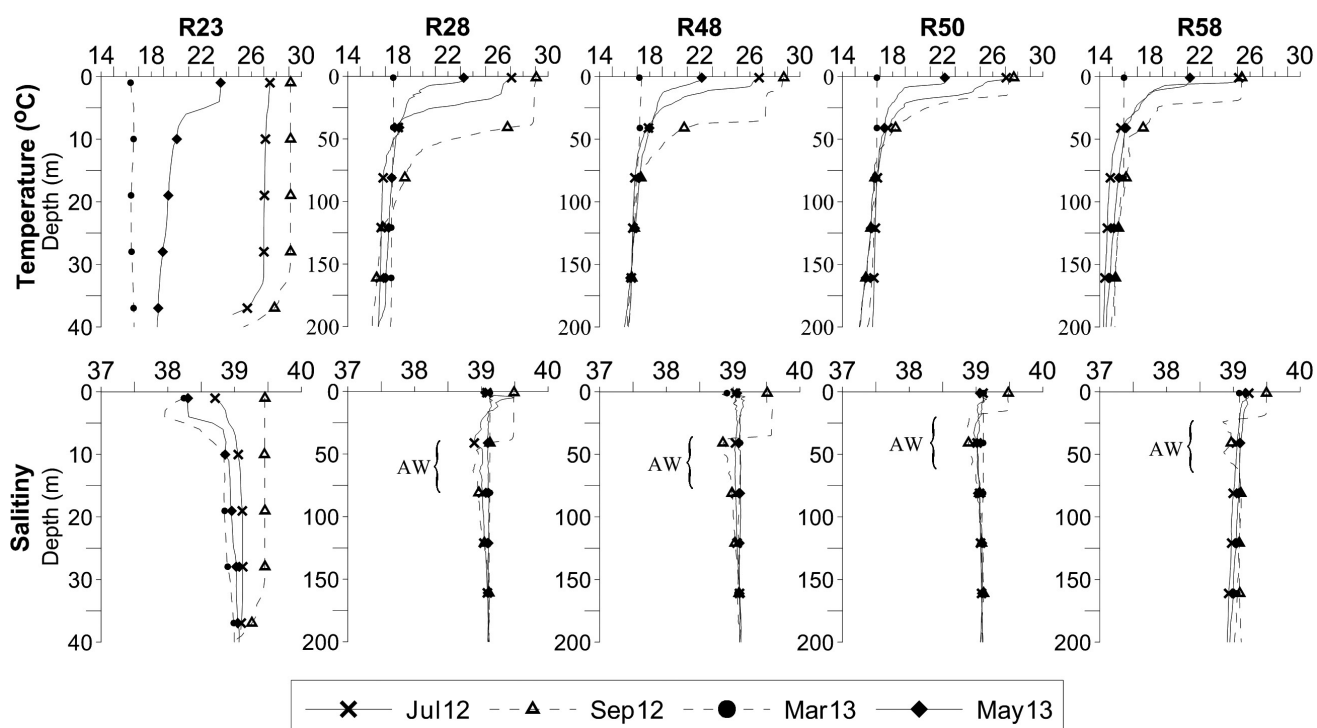


Fig. 2: Temperature and salinity profiles for individual stations and sampling periods (AW: Atlantic water salinity signature detected at all offshore stations (R28-R58) in September 2012).

Table 2. Range of bio-physico-chemical variables (mean, minimum and maximum values) in the study area.

Parameters	R23	R28	R48	R50	R58
Temperature (°C)	23.00 (16.34-29.13)	18.34 (16.00-29.03)	17.73 (15.98-28.71)	17.14 (15.34-27.66)	15.91 (14.30-25.34)
Salinity	39.03 (37.95-39.45)	39.10 (38.87-39.49)	39.09 (38.82-39.59)	39.07 (38.87-39.51)	39.06 (38.84-39.50)
NO ₃ +NO ₂ (μM)	0.45 (0.05-2.66)	0.39 (0.05-2.48)	0.39 (0.05-2.41)	0.60 (0.05-3.82)	1.18 (0.05-5.51)
PO ₄ (μM)	0.03 (0.02-0.07)	0.03 (0.02-0.07)	0.03 (0.02-0.08)	0.04 (0.02-0.13)	0.04 (0.02-0.17)
Chl- <i>a</i> ($\mu\text{g l}^{-1}$)	0.190 (0.025-0.566)	0.047 (0.006-0.160)	0.034 (0.004-0.179)	0.028 (0.004-0.128)	0.069 (0.005-0.401)
Bact. Abundance (10 ⁵ cells ml ⁻¹)	4.5 (2.4-7.3)	2.5 (0.27-4.8)	1.9 (0.21-3.9)	1.6 (0.18-3.0)	1.6 (0.21-6.4)
Bact. Production ($\mu\text{g C l}^{-1} \text{d}^{-1}$)	0.432 (0.009-1.075)	0.185 (0.005-1.384)	0.132 (0.003-0.551)	0.059 (0.003-0.160)	0.077 (0.004-0.246)
Depth Integrated Bact. Production ($\mu\text{g C.m}^{-2}.\text{d}^{-1}$)	15.655 (7.71-22.24)	29.685 (6.09-90.29)	16.077 (9.45-32.76)	9.830 (7.04-14.31)	10.041 (6.71-13.49)
Mean Depth Integrated Bact. Production ($\mu\text{g C.m}^{-3}.\text{d}^{-1}$)	0.401 (0.197-0.570)	0.148 (0.030-0.451)	0.080 (0.047-0.164)	0.049 (0.035-0.071)	0.050 (0.033-0.067)

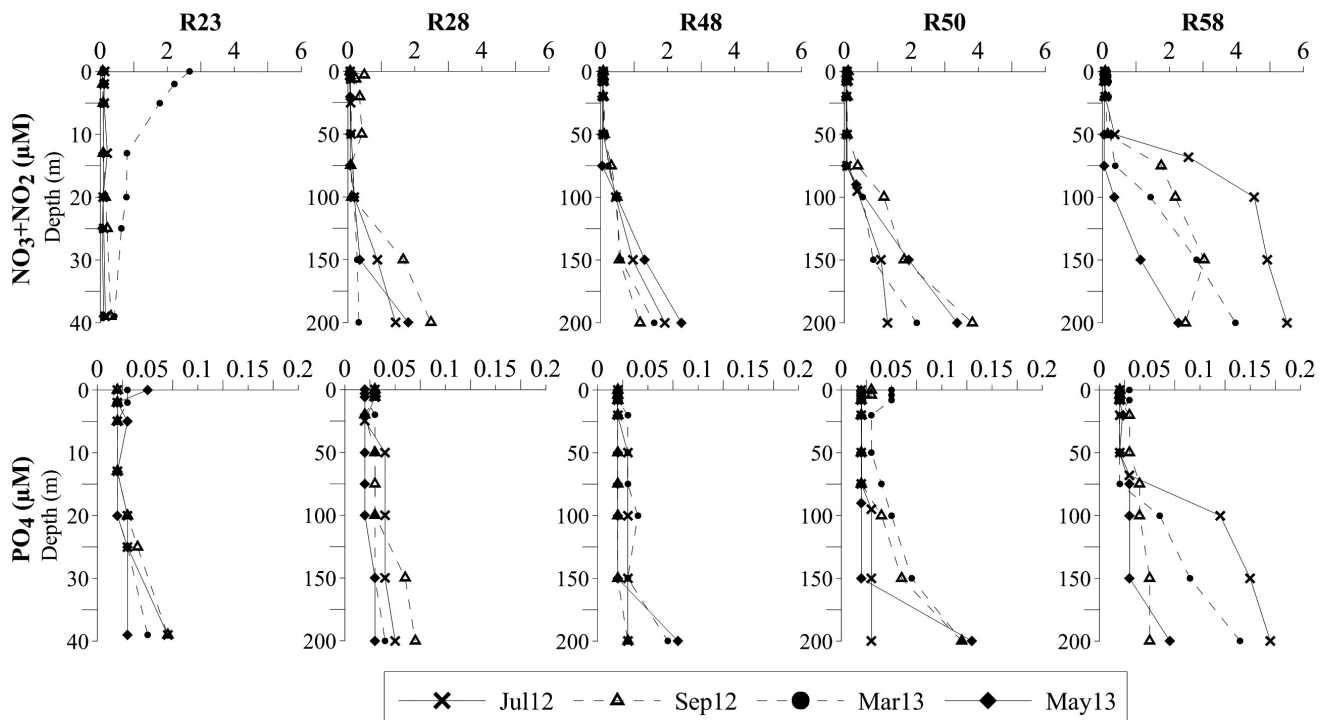


Fig. 3: Nitrate+nitrite and phosphate profiles for individual stations and sampling periods.

Chlorophyll *a*, Bacterial Abundance and Bacterial Production

Chl-*a* concentrations fluctuated between 0.004 and 0.566 $\mu\text{g l}^{-1}$ in the study area (Fig. 4). Chl-*a* content of surface waters reached to a peak at coastal station R23 in March. Very low values were observed below the euphotic layer. Higher concentrations were measured near surface in March 2013. In general, concentrations of Chl *a* were lower than 0.1 $\mu\text{g l}^{-1}$ at offshore stations (Fig. 4). A Deep Chlorophyll Maximum (DCM) was observed between 50 and 100 meters. However DCM became shallower moving westward towards the cyclonic Rhodes Gyre area (Fig. 4).

Bacterial abundance (BA) ranged between 0.18 and 7.3×10^5 cells ml^{-1} during the study period (Fig. 4 and Table 2). While higher values were observed in July 2012, low BA values were recorded in March 2013 in the euphotic layer. BA decreased with increasing depth except at st. R23. Changes in depth dependent abundance were minor at the shallow coastal station R23. Bacterial numbers in the water column tended to decrease westward, although they increased again in proximity of the cyclonic Rhodes Gyre area (Fig. 4, st. R58).

The rate of Bacterial Production (BP) varied in the range of 0.003-1.384 $\mu\text{g C l}^{-1} \text{d}^{-1}$, and the highest activity was observed near the bottom at st. R28 (Fig.4 and Table 2). BP generally decreased with increasing depth in the study area. Low values ($<0.2 \mu\text{g C l}^{-1} \text{d}^{-1}$) were observed in July 2012, March and May 2013 at st. R28 (Fig. 4). Although the activity was high in offshore waters during

September, it was high in the shelf during summer. It was observed that the depth of the productive layer increased towards west (Fig. 4).

Mean Depth Integrated Bacterial Production (M-DIBP) decreased from east to west (from 0.401 to 0.050 $\mu\text{g C m}^{-3} \text{d}^{-1}$) throughout the study period (Fig. 5, axis y2-B). While the highest rates were observed in September 2012 in offshore stations, it was observed in shelf in July 2012 (Fig. 5, axis y1-A). DIBP ranged from 6.09 to 90.29 $\mu\text{g C m}^{-2} \text{d}^{-1}$ throughout the study period (Fig. 5 and Table 2). Both the highest and the lowest rates were measured at st. R28 in September 2012 and March 2013, respectively.

Principal Component Analysis (PCA)

Environmental variables were analyzed using the Principal Component Analysis. The first 2 components accounted for 64.23% of the total variation (Table 3). PCA plot of abiotic and biotic variables (Fig. 6) showed that the temperature was closely related with bacterial abundance and production, which were affected by the level of nutrient at the least. Although there was a considerable affect of Chl-*a* and salinity, they were opposing each other on the plot. According to cluster analysis, R23 separated from other stations with high bacterial production and abundance which may correspond to high freshwater flux. Temperature affected bacterial production and abundance more than salinity and PO_4 and NO_3+NO_2 .

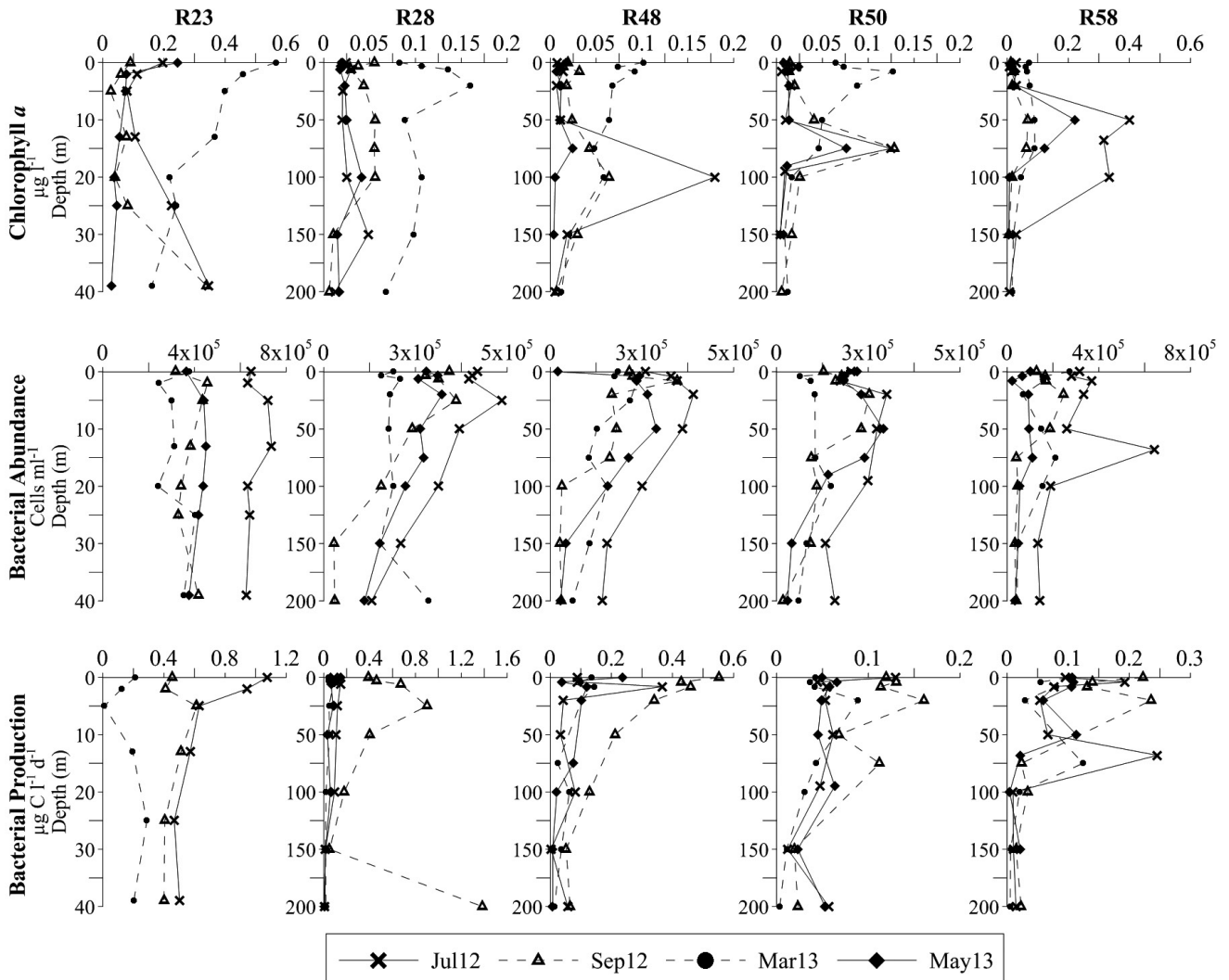


Fig. 4: Chlorophyll, bacterial abundance and bacterial production profiles (note that scales are not the same for each variable across the stations).

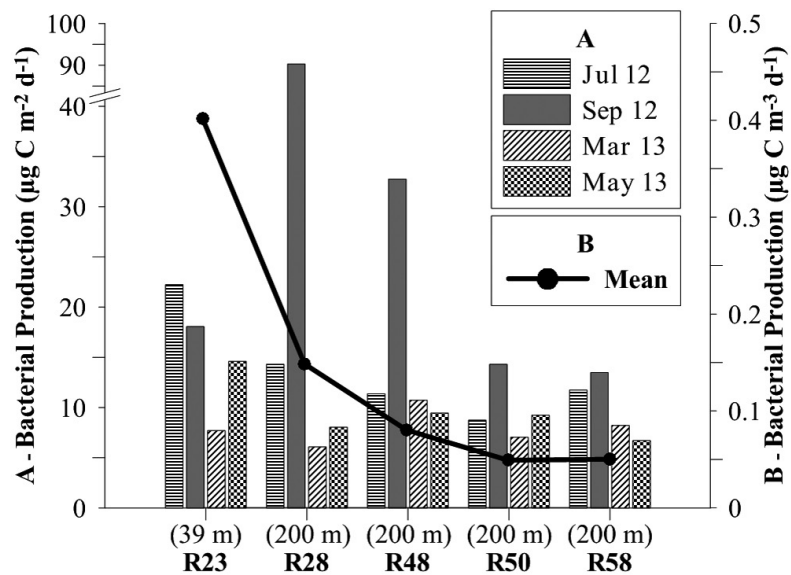


Fig. 5: Rate of depth integrated bacterial production (DIBP- $\mu\text{g C m}^{-2} \text{d}^{-1}$, axis y1-A) and mean ($\mu\text{g C m}^{-3} \text{d}^{-1}$, axis y2-B).

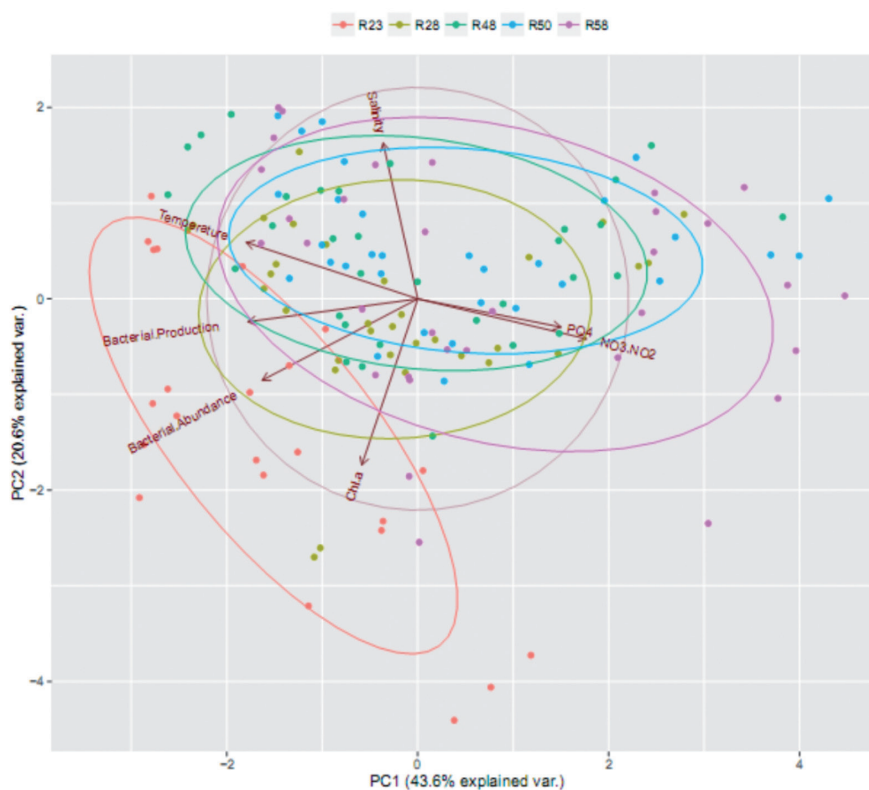


Fig. 6: Principal Component Analysis and Cluster analysis (Ward method-colored circles) of abiotic and biotic variables.

Table 3. Eigenvalues and corresponding values of percentage of variance for each component.

Component	Standard Deviation	Initial Eigenvalues	
		% of Variance	Cumulative %
1	1.7467	43.59	43.59
2	1.2021	20.64	64.23
3	0.9471	12.81	77.04
4	0.77955	8.681	85.72
5	0.67897	6.586	92.31
6	0.56942	4.632	96.94
7	0.46264	3.058	100.00

Extraction Method:Principal Component Analysis

Discussion

In this study, bacterial production (BP) was shown to increase eastward from the northeastern end of the Levantine Basin towards the Rhodes Gyre (Fig. 5). Previously, Siokou-Frangou *et al.* (2010) concluded that an increase in oligotrophic status and a decrease in bacterial production was evident eastward across the Mediterranean basin. However results of the present study show that the influence of particular hydrographic conditions can create contradictions to these ‘grand picture’ at a lower scale. Nonetheless, the present data still show that BP in eastern Mediterranean is quite lower than in the western part of the Mediterranean, with BP

ranges of 0.0048-1.96 and 0.02-7.2 $\mu\text{g C l}^{-1} \text{d}^{-1}$ and BA ranges of $0.4-15.2 \times 10^5$ and $1.5-15 \times 10^5$ cells ml^{-1} in the two sub-basins, respectively (Siokou-Frangou *et al.*, 2010; Raveh *et al.*, 2015).

In fact, the data and the results presented here are the first report of spatial and temporal variations in BP for the region and the trend in the region contradicts previous findings. The main reason of this inconsistency in the spatial trend of BP could be the inclusion of this new study area where the Northeastern sector of Mediterranean basin receives substantial amount of freshwater which further promotes algal growth in shelf waters (Koçak *et al.* 2010). In accord with increasing nutrient flux during winter and spring algal distribution area in the shelf

extends towards offshore and becomes diluted further along its westward route by prevailing current regime (Asia Minor Current, see Fig. 1) in offshore waters. Evidentially, there is a close link between the amount of freshwater flux into the shelf and bacterial biomass in the basin (Yucel, 2013). Higher production rates measured in shelf waters in this study could either be related to the nutrient availability or elevated dissolved organic carbon content of shelf waters or both (Amon & Benner, 1994; Beman *et al.*, 2005; Van Wambeke *et al.*, 2008; Tsai *et al.*, 2011; Yucel 2013; Raveh *et al.*, 2015).

Bacterial abundance (BA) and production (BP) were found to be high after the phytoplankton blooms in spring. Such blooms lead to increase in dissolved organic matters concentration in the water column (Van Wambeke *et al.*, 2008). Bacterial activity is further stimulated with increasing temperature towards summer to autumn as a result of consumption of available DOC originated from the winter-spring algal growth in shelf waters of the Cilician Basin-the northern Levantine Sea (Amon & Benner, 1994; Ducklow, 2000; Turley *et al.*, 2000). Although the highest BAs were observed in July 2012 and the highest BP rates were measured in September 2012 in offshore waters, a significant relation was found between them; however, they do not mimic each other (Adams *et al.*, 2010). Depending on time and space, cells may show different individual growth rates and a population may retain different percentage of active populations (Van Wambeke *et al.*, 2008; Adams *et al.*, 2010). In agreement with the results of this study, Shiah & Ducklow (1994) showed that temperature was more important than other variables (i.e. dissolved nutrients and DOC) as it affected enzymatic activity and affinity to DOC. Kirchman & Rich (1997) found that bacteria respond more quickly to addition of dissolved organic matter at high temperature.

The relation between BA, BP and temperature was obvious throughout the study period (Fig. 6 and Table 3). There was a two-modal pattern of Bacterial production and abundance in July and September 2012 with high sea water temperature (Fig. 2 and Fig. 4). Hence, it is clearly evident that temperature acts as the key parameter regulating bacterial growth (Shiah & Ducklow, 1994; Pomeroy & Wiebe, 2001; Uysal *et al.*, 2004; Tsai *et al.*, 2008; Azaro *et al.*, 2012; Yucel 2013; Raveh *et al.*, 2015).

The range of bacterial abundance values found in this study (0.18 to 7.3×10^5 cells ml^{-1}) is wider than those provided earlier (0.4 to 3.9×10^5 cells ml^{-1}) for the eastern Mediterranean (Robarts *et al.*, 1996). Lower abundances were found in offshore waters than in shelf waters of northern Levantine Sea. BA decreased with increasing oligotrophy towards west except cyclonic Rhodes Gyre. Although pronounced increases in nutrient and Chl-*a* contents of coastal waters were observed in March, there was no increase in bacterial activity. This may be due to either low temperatures or nutrient limitations or interactions of both factors on bacterial activity. Bacteria

can co-exist with several phytoplankton species that may have different nutrient affinity and strategy. When such autotrophic organisms compete for available nutrients, they can also shape bacterial nutrient environment in the water column (Sala *et al.*, 2002; Van Wambeke *et al.*, 2002; Michelou *et al.*, 2011). Raveh *et al.* (2015) reported low bacterial abundance and activity in spring in coastal waters of Tel Shikmona (Haifa), the southern Levantine Sea. They claimed positive linear correlation between bacterial production and primary production which is a source of carbon for bacteria.

Proximity of stations R28 and R48 to the productive shelf waters aided exchange of available nutrients and DOC already formed in the shelf area via the westward meandering Asia Minor boundary Current. Nutrients might have been used more efficiently relative to dissolved organics along the currents (Azam *et al.*, 1983; Robarts *et al.*, 1996; Van Wambeke *et al.*, 2000). Although nutrient supply increased in spring and winter, temperature can limit bacterial abundance (Shiah & Ducklow, 1994). Nevertheless, increasing temperature and dissolved organic matter after winter and spring bloom periods caused higher bacterial abundance although concentration of nutrients decreased in summer and autumn. Raveh *et al.* (2015) found that higher bacterial activity occurred in winter season when dissolved nutrients were high. However, they did not find any relationships between bacterial and primary production in coastal waters, where bacteria depend less on phytoplankton as a source of carbon in contrast to the open Levantine Basin.

Phosphorus levels were generally found to limit bacterial growth, whereas nitrogen limitation or co-limitation also occurs in Mediterranean (Sala *et al.*, 2002; Van Wambeke *et al.*, 2002; Yucel, 2013). The highest bacterial production ($1.384 \mu g C l^{-1} d^{-1}$) and lowest abundance (0.27×10^5 cells ml^{-1}) were recorded at st. R28 at 200 m in September 2012 where nitrate+nitrite and phosphate concentrations reached peak levels of 2.48 and 0.07 μM , respectively. Such high nutrient levels might have stimulated bacterial activity although an opposite relationship between dissolved nutrients (phosphate and nitrite+nitrate) and bacterial production and abundance was found as a general result in our analysis. Type of limiting nutrient may change within short intervals in nature where situation can change quickly (Sala *et al.*, 2002). Besides, microbial groups can utilize different nutrient source in changing situations (Morán *et al.*, 2010).

The depth of the productive layer decreased towards the cyclonic Rhodes Gyre (0-100). Nutrient concentrations and biological activity (Chl-*a* concentration, bacterial abundance and production) increased in the Rhodes Gyre area. This could be because nutrients are transferred to the euphotic zone in this area by upwelling events which result in further promotion of both phytoplankton and bacterial production. Yılmaz & Tuğrul (1998) showed

vertical and horizontal distribution of dissolved nutrients with similar concentrations as those measured in this study in the northern Levantine Sea. Nutrient distribution and amount of microbial production (i.e. primary production) are determined by mixing and eddies in the Levantine Basin. Also, they reported that Levantine deep water (LDW) originated from Atlantic water is less saline and goes up towards west in the Cilician Basin and it reaches to surface in Rhodes Gyre. LDW separates upper water column and deep waters with strong halocline in summer season (Fig. 2). LDW including high nutrient content stimulates primary production in the euphotic layer

Conclusions

This study constitutes the first evaluation of the bacterial production and its relationships with biological and physicochemical parameters in the Levantine Basin. Results highlighted a trend decreasing westward in bacterial activity in the study area. Prevailing current regime transports westward both the suspended particulates and dissolved organics of highly productive shelf waters in this direction. Increased bacterial activity is observed in summer and fall following winter and spring phytoplankton blooms. Furthermore, increase in temperature stimulates bacterial activity, which is strongly limited in the northern Levantine Sea offshore waters by the low amount of dissolved organic matter. This study can help to understand the role of the heterotrophic bacteria in the system and provide data for model studies in the area. Further studies should include dissolved organic carbon estimates together with rate measurements.

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