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Factors affecting the distribution of two *Synechococcus* ecotypes in the coastal Adriatic Sea

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Distribution and abundance of two Synechococcus *ecotypes, phycocyanin-rich cells (PC-SYN) and phycoerythrin-rich cells (PE-SYN) were studied in the surface layer of the central Adriatic Sea during the 2015-2016 period. The studied area included several estuarine areas, and coastal to open sea trophic gradients, covering a wide range of seawater temperatures (11.82 - 20.75^{o}C), salinity (4.47 - 38.84) and nutrient concentration. The abundance of PC-SYN ranged from 0 to 79.79 x 10^3 cell mL^{-1} and that of PE-SYN from 5.01 x 10^3 to 76.74 x 10^3 cell mL^{-1}. Both ecotypes coexisted in the studied waters with PC-SYN cells dominating during spring and PE-SYN during winter and autumn. PC-SYN showed a significant positive relationship with temperature and strong positive responses to nitrogen nutrients, whereas PE-SYN positively responded to phosphate availability. The relative ratio of phosphorus availability and total inorganic nitrogen nutrients (N/P ratio) affects the spatial distribution of the two* Synechococcus *ecotypes.*

Key words: phycocyanin-rich cells, phycoerythrin-rich cells, nitrogen, phosphorus, trophic status

INTRODUCTION

The marine cyanobacteria *Synechococcus* play an important role in global oceanic primary production (PLATT *et al*., 1983; CAMPBELL *et al*., 1994; LIU *et al*., 1998; RICHARDSON & JACKSON, 2007; LOMAS & MORAN, 2011), forming the base of the marine food web (DREBES, 1974; MEDLIN *et al*., 1991). *Synechococcus* species have the ability to acquire nutrients from the sub-micromolar concentrations found in the environment and their light-harvesting system is uniquely adapted to the spectral distribution of light in the marine environment. *Synechococcus* harbours the largest pigment diversity allowing it to exploit a wide range of light niches (HUMILY *et al*., 2013), from turbid coastal waters to the most transparent waters of the open ocean (OLSON *et al*., 1990; WOOD *et al*., 1998; HAVERKAMP *et al*., 2008). It is well-known that all *Synechococcus* species contain phycocyanin (PC) while some also contain phycoerythrin (PE). PC-rich cells (PC-SYN) absorb red light, have a blue-green colour and penetrate deep into the water column (OLSON *et al*., 1990) or can dominate in turbid waters, such as estuarine, where red light prevails (STOMP *et al*., 2007). PE-rich cells (PE-SYN) absorb green light, have a red appearance and dominate in oceanic waters (OLSON *et al*., 1990; WOOD *et al*., 1998; SCANLAN *et al*., 2003).

The significant contribution of *Synechococcus* to the total biomass and primary production has been reported for the open Adriatic Sea (RADIĆ *et al*., 2009; ŠANTIĆ *et al*., 2013; ŠANTIĆ *et al*., 2014; ŠOLIĆ *et al*., 2015). A recent study indicates that they can also constitute an important component of coastal and estuarine waters (ŠOLIĆ *et al*., 2015). The previous studies in the Adriatic Sea were focused on total *Synechococcus* abundance (NINČEVIĆ GLADAN *et al*., 2006; ŠANTIĆ *et al*., 2011; ŠANTIĆ *et al*., 2013; ŠANTIĆ *et al*., 2014), while no distinction was made between these two types of *Synechococcus* cells.

The aim of this study was to examine the abundance of PC-SYN and PE-SYN cells along the central and southern Adriatic coast and to determine the environmental conditions that favour the occurrence and abundance of these two types of cells. We hypothesized that phosphorus limitation in the study area and the difference in the relative availability of phosphorus and nitrogen nutrients affect the spatial distribution and abundance of the two *Synechococcus* ecotypes.

MATERIAL AND METHODS

Sampling locations

Sampling was performed in May and November 2015 at 11 stations located along the central and southern part of the eastern Adriatic coast (Fig. 1 & Fig. 2). Stations were grouped in the areas that are under strong influence of the Krka River (stations K1-K3); Jadro River (stations J1-J2); Neretva River (stations N1-N4), Ombla River (station O1) and an area near the Island of Pag that is temporally influenced by underwater springs (station P1). Another four stations (A1-A4) forming a transect line from the coastal area to the open sea, following the trophic gradient, were sampled more frequently (February, March, April, May, November and December 2015, and January 2016). All samples were collected from the surface layer using Niskin bottles (5 L).

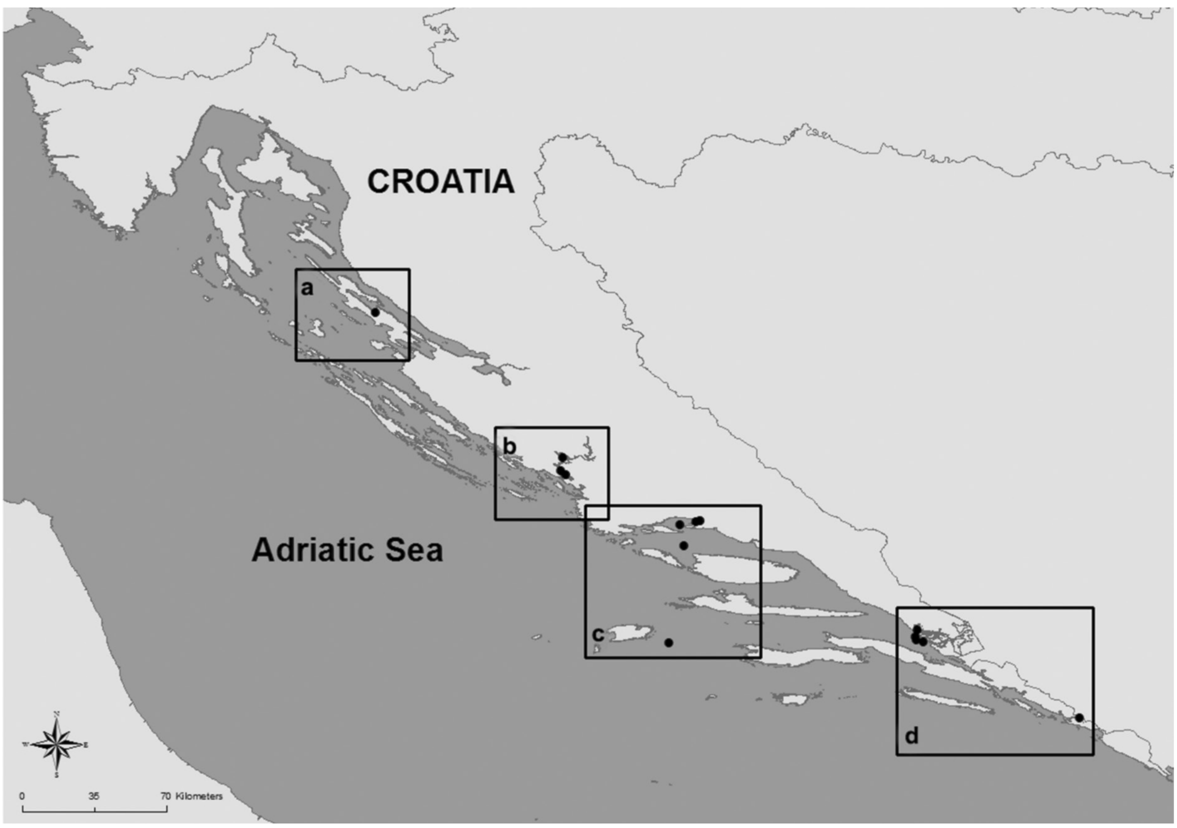

Fig. 1. Adriatic Sea with studied areas

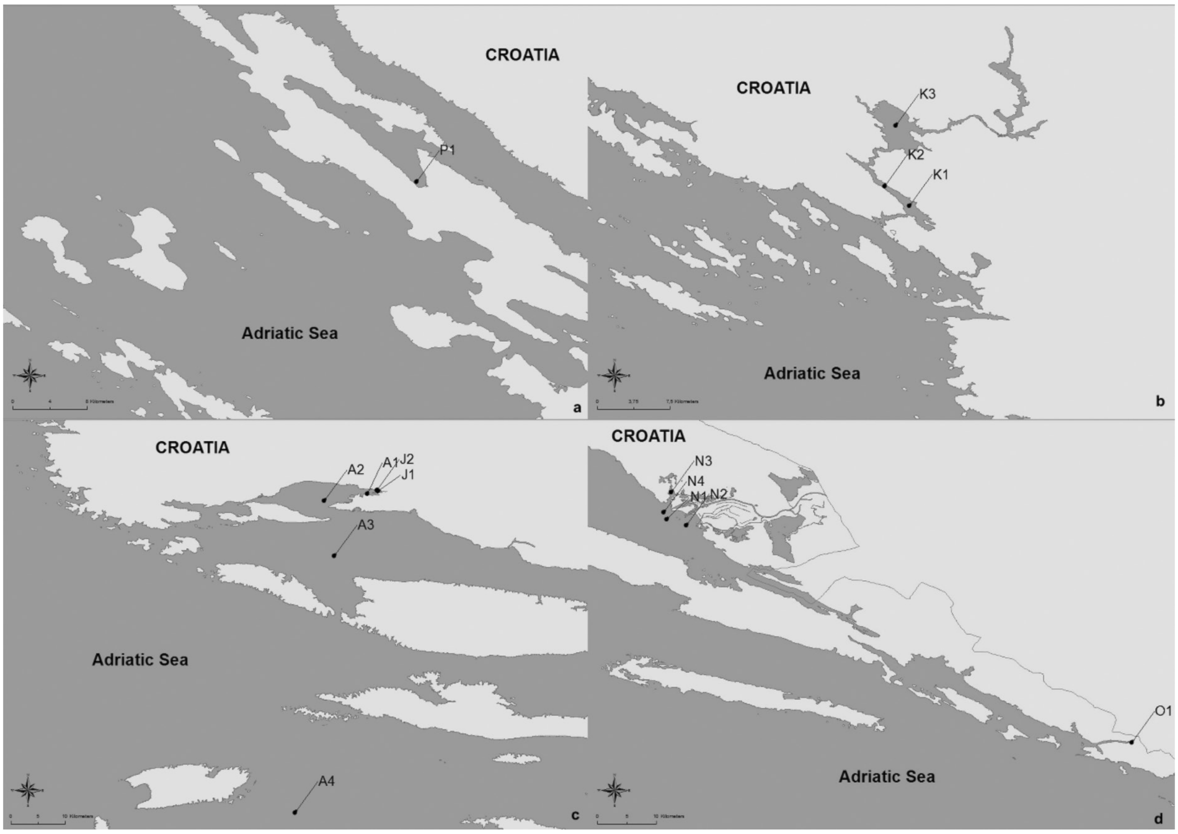

Fig. 2. Studied area with sampling locations

Data collection

A SeaBird 25 CTD profiler recorded temperature and salinity data. Nutrient concentration (ammonium ion/NH_4^+; nitrate ion/NO_3^-; nitrite ion/NO_2^- and soluble reactive phosphorus/SRP) were determined in unfiltered samples using the autoanalyser-modified method by GRASSHOF (1976). Chlorophyll *a* (*Chl a*) was determined from 500-mL sub-samples filtered through Whatman GF/F glass-fibre filters stored at -20°C. These were homogenized and extracted in 90% acetone. Samples were analysed fluorometrically with a Turner TD-700 Laboratory Fluorometer calibrated with pure *Chl a* (Sigma) (Strickland and Parsons, 1972).

The abundance of phycoerythrin-rich cells (PE-SYN) and phycocyanin-rich cells (PC-SYN) was determined using epifluorescence microscopy (RAY *et al.*, 1989). Samples were preserved in 2% formaldehyde and stored at 4˚C until analysis. The preserved samples (5 mL to 15 mL) were filtered through black 0.2 µm pore-size Nuclepore filters (25 mm diameter). Filters were processed using an Olympus BX51 with standard blue and green filter combinations. Under blue excitation (450-490 nm, LP 520) PE-SYN fluoresces yellow to orange, while under green excitation (510-560 nm, LP 590) PE-SYN and PC-SYN cells fluoresces red. The difference between the total counts of cyanobacterial cells enumerated under green excitation minus the cell count obtained under blue excitation gives the number of PC-SYN cells. The 30 fields of view were counted at x1000 magnification.

Abundances of SybrGreen I-stained non-pigmented bacteria were determined using flow cytometry (MARIE *et al.*, 1997). Bacterial cell production was measured from DNA synthesis based on incorporation rates of ^{3}H-thymidine (FUHRMAN & AZAM, 1982).

Statistical operations were performed using STATISTICA 8.0 software, and multivariate analyses were performed using CANOCO 5 software (TER BRAAK & ŠMILAUER, 2012).

RESULTS

Spatial and temporal distribution of two *Synechococcus* ecotypes

In general, the abundances of PC-rich *Synechococcus* (PC-SYN) cells were higher in May, whereas PE-rich cells (PE-SYN) showed higher abundance in November (Fig. 3).

Average abundance of PC-SYN in May was 29.92 ±16.45 x 10^3 cell mL^{-1}, and ranged between 5.63 x 10^3 cell mL^{-1} in the Ombla estuary area, and 35.72±38.18 x 10^3 cell mL^{-1} in the Krka estuary area. In November, average abundance of PC-SYN was 18.28±11.46 x 10^3 cell mL^{-1}, and ranged from 4.85 x 10^3 cell mL^{-1} in the Ombla estuary area to 28.66±2.99 x 10^3 cell mL^{-1} in the Jadro estuary area.

Average abundance of PE-SYN in May was 22.61±12.27 x 10^3 cell mL^{-1}, and ranged between 6.61 x 10^3 cell mL^{-1} in the Island of Pag area, and 32.52±14.55 x 10^3 cell mL^{-1} in the Jadro estuary area. In November, average abundance of PE-SYN was 39.53±19.97 x 10^3 cell mL^{-1}, and ranged from 13.58±3.48 x 10^3 cell mL^{-1} in the Krka estuary area to 64.38±13.93 x 10^3 cell mL^{-1} in the Jadro estuary area.

PE-SYN abundance dominated over PC-SYN abundance in the Jadro, Neretva and Ombla estuaries during both studied periods, with more expressed domination in November. Domination of PC-SYN over PE-SYN cells was found in the Krka estuary during both periods. Finally, in the area around Pag Island, PC-SYN dominated over PE-SYN in May, while during November the reverse situation was found.

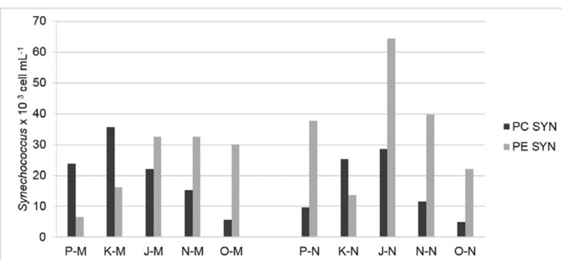

Fig. 3. Distribution of PE-rich (PE-SYN) and PC-rich (PC-SYN) Synechococcus *cells along investigated areas Pag Island (P), Krka estuary (K), Jadro estuary (J), Neretva estuary (N) and Ombla estuary (O) during May (M) and November (N) 2015*

Decreasing trends of PC-SYN and PE-SYN abundances along the trophic gradient, from the coastal area (A1) to the open sea (A4) were established (Fig. 4). Considering seasonally, it appears that abundance of PC-SYN dominated over PE-SYN during the spring period, whereas PE-SYN cells dominated during winter and autumn.

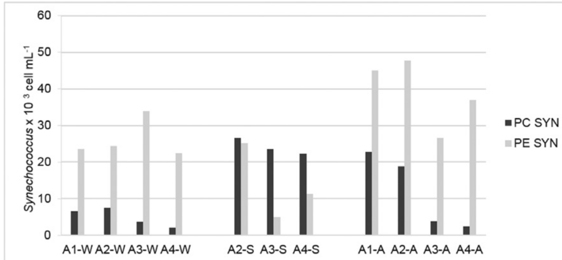

Fig. 4. Seasonal distribution of PE-rich (PE-SYN) and PC-rich (PC-SYN) Synechococcus *cells at stations A1, A2, A3 and A4, during winter (W), spring (S) and autumn (A) 2015 and 2016*

Relationship of PC-SYN and PE-SYN abundances with environmental parameters

The distribution and abundance of two types of *Synechococcus* cells were investigated over a wide range of abiotic (temperature, salinity, inorganic nutrients and chlorophyll) and biotic (bacterial abundance, bacterial production) environmental conditions (Table 1). This gave us the opportunity to analyse the environmental conditions that favour the occurrence and abundance of these two types of cell. For this purpose, we used the Redundancy Analysis method (RDA) to extract and summarise the variation for a set of response variables that can be explained by a set of explanatory variables. More specifically, RDA is a direct gradient analysis technique, which summarises linear relationships between components of response variables that are "explained" by a set of explanatory variables. In our case, RDA summarizes the part of the variation in PC-SYN and PE-SYN abundances explained by environmental variables (Fig. 5). The abundance of heterotrophic bacteria and bacterial production were also included in the analysis, as response variables.

Table 1. Minimum and maximum values of biotic and abiotic parameters along the studied area. BA – bacterial abundance (x10^6 cells mL^{-1}); BP – bacterial production (x10^4 cells mL^{-1} h^{-1}); T – temperature (^{o}C); S – salinity; NO_3^-/ nitrate; nitrate ion/NO_3^-; nitrite ion/NO_2^-; ammonium ion/NH_4^+, soluble reactive phosphorus/SRP (µM); N/P ratio and Chl a – chlorophyll a concentration (mg m^{-3})

Area	Range	BA	BP	T	S	NO_3^-	NO_2^-	NH_4^+	SRP	N/P	Chl *a*
Trophic	**Min**	0.24	0.10	11.94	34.93	0.45	0.07	0.08	0.03	5.45	0.14
profile	**Max**	0.92	0.87	20.19	38.84	3.08	0.39	0.81	0.24	94.75	1.34
Ombla	**Min**	0.34	0.26	14.07	5.44	34.16	0.07	0.2	0.20	86.66	0.01
	Max	0.43	0.27	15.09	11.14	38.31	0.16	1.11	0.41	197.23	0.1
Jadro	**Min**	0.53	0.26	16.33	32.85	1.98	0.16	0.42	0.02	24.74	0.4
	Max	1.03	0.57	20.75	37.83	27.39	0.53	2.74	0.42	127.48	0.88
Krka	**Min**	0.11	0.23	11.82	4.47	14.99	0.12	0.37	0.02	175.94	0.55
	Max	2.14	0.74	20.19	24.01	25.15	0.54	2.08	0.14	797.78	2.21
Pag	**Min**	0.33	0.27	11.92	36.25	0.53	0.04	0.03	0.07	6.71	0.39
	Max	0.55	0.47	17.33	37.36	1.19	0.32	0.96	0.17	28.72	1.13
Neretva	**Min**	0.15	0.26	16.69	34.35	0.18	0.03	0.14	0.01	3.33	0.36
	Max	0.71	0.44	19.30	37.67	3.19	0.26	0.68	0.10	656.33	0.84

The first and second axes accounted for 42.69 % of the observed variance in the studied picoplankton community. Most of the variance was explained by *Chl a* concentration (16.6%; pseudo-F = 7.0; P<0.01), temperature (12.9%; pseudo-F = 5.2; P<0.01) and N/P ratio (12.3%; pseudo-F = 4.9; P<0.01). The arrows on the RDA ordination plot indicate the direction of the steepest increase of the respective variable and the angles between two lines reflect correlations between respective variables. The result of RDA analysis pointed to temperature and nutrients as the environmental factors most responsible for the differences in the distribution and abundance of two types of *Synechococcus* cells. PC-SYN showed a significant positive relationship with temperature (r = 0.43; P<0.01), whereas PE-SYN did not correlate with temperature. Furthermore, PC-SYN showed strong positive responses to nitrogen nutrients, whereas PE-SYN positively responded to the availability of phosphates (the correlation coefficient with phosphate was 0.46; P<0.01). The relative ratio of phosphorus availability and nitrogen nutrients (N/P ratio) affects the spatial distribution and abundance of the two *Synechococcus* ecotypes. An increasing N/P ratio was accompanied by an increase of PC-SYN cells (r = 0.36; P<0.05), whereas PE-SYN showed no correlation with the N/P ratio.

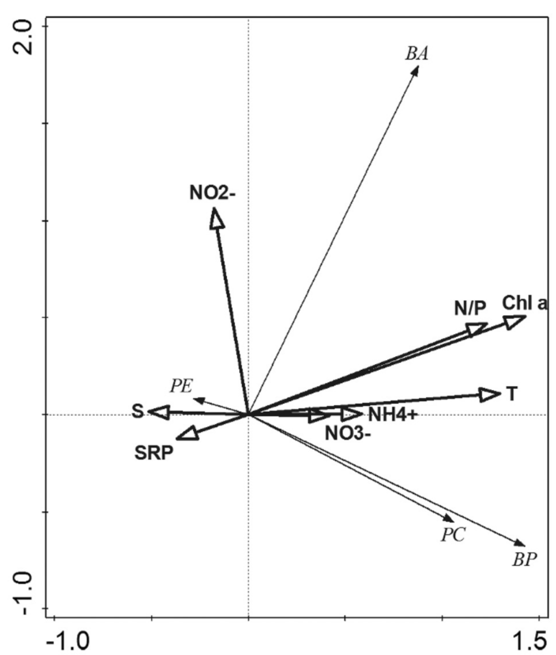

Fig. 5. Redundancy analysis (RDA) biplot of PC-SYN (PC) and PE-SYN (PE) abundances, bacterial abundance (BA) and bacterial production (BP) and environmental parameters (T – temperature, S – salinity; NO_3^-/ nitrate ion; NO_2^-/nitrite ion; NH_4^+/ammonium ion; SRP/soluble reactive phosphorus; N/P ratio and Chl a – chlorophyll a concentration)

DISCUSSION

Salinity has been reported as the most important factor in determining the distribution of different *Synechococcus* ecotypes in marine and estuarine ecosystems. Some authors have shown that PC-SYN cells were abundant in low salinity waters, whereas the PE-SYN cells were abundant in high salinity waters (RAJANEESH & MITBAVKAR, 2013; HASS & PEARL, 1988; ZHANG *et al*., 2013). On the contrary, other studies have identified the coexistence of these two ecotypes in estuaries, coastal and fresh waters (MURRELL & LORES, 2004; STOMP *et al*., 2007; HAVERKAMP *et al*., 2008). Although our study showed a dominance of PC-SYN over PE-SYN cells in the Krka estuary, this pattern was not common throughout the study area. Moreover, our results show that both types of cell were distributed along a wide range of salinity (from 4.47 to 38.84), which is in accordance with reports that PC-SYN cells are extremely halotolerant (WATERBURY *et al*., 1986; RAJANEESH & MITBAVKAR, 2013).

In this study PC-SYN and bacterial production showed a positive relationship with *Chl a* and nitrogen nutrients in the surface layer, indicating their preference for more eutrophic environments (SEITZINGER & SANDERS, 1997), regardless of salinity. The typical feature of the studied estuaries is phosphorus limitation but not nitrogen, which is a consequence of the fact that the eastern Adriatic karstic rivers carry small amounts of phosphorus (UNEP/MAP, 2003; *ŠOLIĆ et al*., 2015). Therefore, these conditions stimulate the growth of PC-SYN cells, which generally dominated over PE-SYN cells in the studied estuarine areas. Nitrogen is an important ecological controlling factor of marine microbes, because of its concentration and form that varies in marine ecosystems (DORE & KARL, 1996; LIPSCHULTZ, 2001). Marine *Synechococcus* strains cannot fix N_2 but they are capable of using a wide variety of organic (urea and amino acids) and inorganic (ammonium, nitrite and nitrate) nitrogen sources (GILBERT *et al*., 1986; MOORE *et al*., 2002; FULLER *et al*., 2003; PALENIK *et al*., 2003; AHLGREN & ROCAP, 2006; QIU *et al*., 2010; ZHANG *et al*., 2013). A recent study showed that the 16 clades of *Synechococcus* include fully separate ecotypes that consume only one N-compound type (nitrite, nitrate or ammonium) and represent ecologically distinct populations or ecotypes (AHLGREN & ROCAP, 2006). A laboratory experiment showed that PC-SYN cells grow well in high nitrate and phosphate concentrations, whereas PE-SYN cells cannot tolerate high nitrate concentrations (ERNST *et al*., 2005). NINČEVIĆ GLADAN *et al*. (2006) and ŠOLIĆ *et al*. (2015) demonstrated a clear link between *Synechococcus* abundance and phosphate in the Adriatic Sea, which is characterised by P-limitation. ŠOLIĆ *et al*. (2015) highlight the potential importance of cyanobacteria of the genus *Synechococcus* in phosphorus-limited estuaries, which could be explained by the coexistence of the two ecotypes.

This study showed that both studied *Synechococcus* ecotypes are important components of the microbial communities in the coastal Adriatic Sea. However, different environmental conditions may favour one or the other ecotype. PC-SYN preferred more eutrophic areas over a wide range of salinity. Furthermore, PC-SYN showed a significant positive relationship with temperature, as well in previous studies in the open central (ŠANTIĆ *et al*., 2011) and northern Adriatic Sea (FUKS *et al*., 2005). In addition, our results indicate a strong positive response to nitrogen nutrients, whereas PE-SYN positively responded to the availability of phosphate. The relative ratio of phosphorus availability and nitrogen nutrients (N/P ratio) affects the spatial distribution of the two *Synechococcus* ecotypes.

CONCLUSIONS

Two *Synechococcus* ecotypes PC-SYN and PE-SYN, coexisted in the surface layer of the coastal Adriatic Sea. Whilst PC-SYN cells dominated during spring, PE-SYN dominated during winter and autumn. Furthermore, PC-SYN showed a significant positive relationship with temperature and nitrogen nutrients, whereas PE-SYN showed a positive response to phosphate availability. The spatial distribution of the two *Synechococcus* ecotypes is affected by the relative ratio of phosphorus availability and total inorganic nitrogen nutrients. Also, both ecotypes represent an important component of the microbial community in the coastal Adriatic Sea.

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Utjecaj ekoloških čimbenika na raspodjelu dva ekotipa roda *Synechococcus* u obalnom moru Jadrana

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SAŽETAK

U radu je istražena raspodjela i brojnost dva ekotipa roda *Synechococcus,* tzv. stanice bogate fikocijaninom (PC-SYN) i stanice bogate fikoeritrinom (PE-SYN) u površinskom sloju vodenog stupca, tijekom 2015. i 2016. godine. Područje istraživanja obuhvaćalo je nekoliko estuarijskih područja te područje trofičkog gradijenta od obale prema otvorenom moru, širokog raspona temperature mora (11.82 - 20.75^{o}C), saliniteta (4.47 - 38.84) i koncentracije hranjiva. Brojnost PC-SYN bila je u rasponu od 0 do 79.79 x 10^3 st mL^{-1}, a PE-SYN od 5.01 x 10^3 do 76.74 x 10^3 st mL^{-1}. Utvrđeno je istovremeno obitavanje oba ekotipa na istraživanom području, s prevladavanjem PC-SYN tijekom proljeća te PE-SYN tijekom zime i jeseni. Pokazana je statistički značajna povezanost između PC-SYN i temperature te njegova jaka pozitivna povezanost s dušikovim spojevima, dok su PE-SYN stanice pozitivno odgovorile na dostupnost fosfata. Relativni omjer dostupnosti fosfora i ukupnih hranjiva dušika (N/P omjer) utjecao je na prostornu raspodjelu oba ekotipa roda *Synechococcus*.

Ključne riječi: stanice bogate fikoeritrinom, fikoeritrinom, dušik, fosfor, trofičko stanje