Ecophysiological characteristics of red, green and brown strains of the Baltic picocyanobacterium *Synechococcus* sp. – a laboratory study

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Abstract. The contribution of picocyanobacteria (PCY) to summer phytoplankton blooms, accompanied by an ecological crisis is a new phenomenon in Europe. This issue requires careful investigation. Therefore, the work, which examines the response of *Synechococcus* sp. physiology to different environmental conditions was conducted. Three strains of *Synechococcus* sp. (red BA-120, green BA-124 and brown BA-132) were cultivated in a laboratory under previously determined environmental conditions. These conditions were as follows: temperature (T) from 10 by 5 to 25°C, salinity from 3 by 5 to 18 PSU and Photosynthetically Active Radiation (PAR) from 10 by 90 to 280 μmol photons m^{-2} s^{-1}, which gave 64 combinations of synthetic, though real environmental conditions. Scenarios reflecting all possible combinations were applied in the laboratory experiments. Results pointed to differences in final number of cells between strains. However, there was also a similar pattern for BA-124 and BA-132, which showed the highest concentrations of picocyanobacteria cells at higher T and PAR. This was also the case for BA-120, but only to a certain degree as the number of cells started to decrease above 190 μmol photons m^{-2} s^{-1} PAR. Pigmentation, chlorophyll *a* (Chl *a*), fluorescence and rate of photosynthesis presented both similarities and differences between the strains. In this context, more consistent features were observed for brown and red strains when compared to the green. In this paper are defined the ecophysiological responses of PCY.

1 Introduction

The presence of picoplankton and its contribution to marine biomass were ignored in environmental studies conducted before 1970. This was related to the poor accuracy of research equipment, which did not enable recording and recognition of such small organisms. Before the discovery of picocyanobacteria (PCY) in the oceans by Johnson and Sieburth (1979) and Waterbury et al. (1979) there only existed incidental reports of this fraction of cyanobacteria occurrence in aquatic ecosystems. Since then, the number of PCY observations has rapidly increased, and currently they are known to be present in many marine, brackish and freshwater ecosystems of the world (e.g., Callieri, 2010; Sorokin and Zakuskina, 2010; Flombaum et al., 2013; Jodłowska and Śliwińska, 2014; Jasser and Callieri, 2017). Additionally, recent works showed that many aquatic ecosystems have been experiencing super-dense, long-term blooms of picocyanobacteria (Sorokin et al., 2004; Sorokin and Zakuskina, 2010), whilst in the past PCY were often described as a non-blooming group (Stockner et al., 1988). Sorokin and Zakuskina (2010) found that the picocyanobacteria blooms were accompanied by great changes in the benthic habitats.

Picocyanobacteria of the *Synechococcus* genus are extremely important organisms in the world's oceans. This is the smallest fraction of plankton ranked by the size of cells, which ranges from 0.2 to 2.0 μm (Sieburth et al., 1978). Chrococcoid genus of the *Synechococcus* are ubiquitous components of the natural plankton communities in aquatic environments. Picocyanobacteria of the *Synechococcus* group span a range of different colors, depending on their pigments composition (Stomp et al., 2007; Haverkamp et al., 2008). *Synechococcus* sp. ranged by the pigment content are divided into two main groups: strains rich in the pigment phycoerythrin (PE), rendering the representatives a variety of orange, brown, reddish, pink and purple colors, and strains rich in phycocyanin (PC), coloring the organism in various shades of blue-green (Haverkamp et al., 2009). Baltic strains of *Synechococcus* sp. are classified as three main groups: red and brown strains rich in PE and green strains rich in PC (Mazur-Marzec et al., 2013; Jodłowska and Śliwińska, 2014). The difference between red and brown strains is a proportion of two different bilin pigments known as phycoerythrobilin (PEB) and phycourobilin (PUB), which both bind to the PE apoprotein (Everroad and Wood, 2006; Stomp et al., 2007; Six et al., 2007a, b; Haverkamp et al., 2008; 2009). The three strains of *Synechococcus* sp.: BA-120 (red), BA-124 (green), and BA-132 (brown) examined in this work (Fig. S1 in Supplement) are different morphotypes representatives. Coexistence of PE and PC-rich picocyanobacteria can be found in waters of intermediate turbidity, such as many freshwater lakes and coastal seas including the Baltic Sea (Andersson et al., 1996; Hajdu et al., 2007; Stomp et al., 2007; Haverkamp et al., 2008; Haverkamp et al., 2009; Mazur-Marzec et al., 2013; Larsson et al., 2014; Paczkowska et al., 2017).

Picocyanobacterial species are phylogenetically divided into several major clusters. These clusters have been identified, based on photosynthetic pigmentation, nitrogen requirements, motility and salinity preferences (Herdman et al., 2001). Picocyanobacteria that are found and isolated from marine, brackish and freshwater environments are often related to *Synechococcus* cluster 5 (Herdman et al., 2001). *Synechococcus* cluster 5 is divided in two sub-clusters: 5.1 and 5.2. The members of cluster 5.1 typically produce PE as their main photosynthetic pigment. In contrast, members of cluster 5.2 have a green coloration because they produce PC (Herdman et al., 2001; Larsson et al., 2014). The diversity of PCY has been investigated mainly by analysis of the 16S rRNA gene. However, the phylogenetic tree of *Synechococcus* sp. is not always consistent with their pigmentation type (Haverkamp et al., 2008). Thus, the actual taxonomic position may be incorrectly defined due to the morphological plasticity of these organisms (Callieri, 2010).

Despite its association with open ocean systems, it has become increasingly evident in recent years that *Synechococcus* sp. is a significant contributor to cyanobacterial blooms (Beardall, 2008). Surprisingly, this species may also comprise 80% and more of the total cyanobacterial biomass during cyanobacterial blooms in the Baltic Sea (Stal et al., 2003; Mazur-Marzec et al., 2013).

Recently, it has been confirmed that PCY are able to excrete harmful and allelopathic substances (e.g., Jakubowska and Szeląg-Wasilewska, 2015; Jasser and Callieri, 2017; Śliwińska-Wilczewska et al., 2017; Barreiro Felpeto et al., 2018). Many different factors, including physical parameters, availability and competition for resources, selective grazing and allelopathic interactions can affect the occurrence of harmful blooms in aquatic ecosystems. The development of massive algal blooms is a consequence of the interaction between many favorable factors. *Synechococcus* sp. greatly contributes to these massive blooms, but so far the characteristics of the life cycle of Baltic PCY has not been sufficiently studied. This knowledge needs to be expanded and improved, especially because of bloom toxicity and their negative impacts on ecosystems (Jasser and Callieri, 2017; Śliwińska-Wilczewska et al., 2018a).

According to the all above, phytoplankton is of great interest to scientists in terms of understanding its life cycles and impact on the ecosystem in different parts of the world's oceans and within diverse environmental conditions. In order to investigate it, scientists use various types of research methodology: in-situ measurements, laboratory experiments and numerical estimations. All of these approaches are necessary and essential in marine phytoplankton research. Some laboratory and field studies of ecophysiological responses of picocyanobacteria to different growth conditions have already been completed for typical oceanic mediums, semi-closed seas and lakes (e.g., Glover et al., 1986; Kuosa, 1988; Stal et al., 1999; Agawin et al., 2000; Callieri and Stockner, 2002; Hajdu et al., 2007; Sánchez-Baracaldo et al., 2008; Cai and Kong, 2013; Motwani et al., 2013; Jodłowska and Śliwińska, 2014, Stawiarski et al., 2016). However, there is still a need to provide more systematic information about these organisms. What is more, the need is amplified by the fact that there are only a few research papers on the brown strain of Baltic *Synechococcus* sp. (Stal et al., 2003; Haverkamp et al., 2008; 2009; Jodłowska and Śliwińska, 2014). This gives limited knowledge of PCY and their life cycle in the Baltic Sea, as brown form also contributes to total pico- and phytoplankton biomass in the area of interest (Stal et al., 2003). The above strengthens the motivation to conduct studies on the brown strain of *Synechococcus* sp.

The overall goal of this paper is to determine the most favorable and unfavorable environmental conditions for PCY to grow on the basis of three different strains of *Synechococcus* sp. ecophysiological analysis. What is more, this study aims at describing pigmentation, Chl a fluorescence parameters and photosynthesis performance of PCY cells grown in different environmental conditions. The goal is also to demonstrate how the increasing abundance of PCY in the Baltic Sea may impact the marine ecosystem functioning. The initial step of this study was to carry out laboratory experiments on *Synechococcus* sp. cultures. In order to create different environmental conditions in the Baltic Sea range, combinations of physical quantities were determined. In total, 64 combinations (environmental scenarios) were generated. The second step was to plot and analyze all results after seven days of incubations. For the results, the number of cells, pigmentation, Chl *a* fluorescence parameters, and rate of photosynthesis were collected. The third step was to extract any significant relations between the results and specific physical factors by using a statistical analysis, which included the variance method analysis (two-way ANOVA) and Tukey's HSD post-hoc test. Derived laboratory results help to develop the knowledge on the picocyanobacteria life cycle. Moreover, the PCY experiments underlie the improved numerical approach to phytoplankton modeling development. On the basis of derived results, the algorithms for picocyanobacterium growth is being created in a separate study.

2 Material and methods

2.1 Material and culture conditions

Three different phenotypes of picocyanobacteria strains from the genus *Synechococcus* were examined: BA-120 (red), BA-124 (green), and BA-132 (brown). The *Synechococcus* sp. strains were isolated from the coastal zone of the Gulf of Gdansk (southern Baltic Sea) and maintained as unialgal cultures in the Culture Collection of Baltic Algae (CCBA) at the Institute of Oceanography, University of Gdańsk, Poland (Latała et al., 2006).

The experiments on the 'batch cultures' were carried out in 25 mL glass Erlenmeyer flasks containing sterilized f/2 medium (Guillard, 1975). Culture media was prepared with artificial seawater filtered through a 0.45-μm filters (Macherey-Nagel MN GF-5) using a vacuum pump (600 mbar) and autoclaved. The cultures were incubated in 35 mL Erlenmeyer glass flasks. Salinity of the media was prepared by dissolving Tropic Marine Synthetic Sea Salt in distilled water. The major nutrients, microelements and vitamin concentrations were added according to a method proposed by Guillard (1975) (any of the components in f/2 media were not replaced by Tropic Marine Synthetic Sea Salt).

The PCY cultures were adapted to the various synthetic environmental conditions for two days. The conditions were the combinations of different values of: scalar irradiance in Photosynthetically Active Radiation (PAR) spectrum (10, 100, 190 and 280 μmol photons m^{-2} s^{-1}), temperature (T) (10, 15, 20 and 25°C), and salinity (3, 8, 13 and 18 PSU). The salinity was controlled by salinometer (inoLab Cond Level 1, Weilheim in Oberbayern, Germany). The intensity of PAR was measured using a LI-COR spherical quantum-meter (LI-189, LI-COR Inc., Nebraska, USA). Fluorescent lamps (Cool White 40W, Sylvania, USA) were used as source of irradiance and combined with halogen lamps (100W, Sylvania, USA) to obtain more intensive light. Both light sources give PAR spectrum. This was proved by Jodłowska and Latała (2010) and Jodłowska and Śliwińska (2014). What is more, LI-COR manual with technical specification therein, says that the sensor first checks the light spectrum and if it responds PAR spectrum, the intensity of radiation is measured. This implies, all the results given by LI-COR refers to PAR. Values of quantities representing each environmental condition were applied at the fixed intervals, i.e.: PAR, interval 90; T, interval 5; salinity, interval 5.

The synthetic environmental conditions of salinity and T applied in the laboratory are representative for the Baltic Sea area (Feistelet al., 2008; 2009; Siegel and Gerth, 2017). Moreover, the values of environmental conditions variables (salinity, temperature, PAR) were also specified in certain ranges to make this study comparable with other laboratory cultures experiments available in literature. The combination of the quantities of environmental variables is called a scenario in the present paper. After acclimation time (2 d), the PCY cells served as inoculum for the right test cultures with the initial number of cells equal to 10^6 cells mL^{-1}. The flasks with picocyanobacteria were shaken (once a day) during the experiment. In order to achieve the most reliable results, test cultures were grown in three replicas and were incubated for one week at each combination of light, temperature and salinity. On the last day of incubation the number of cells, pigment content, Chl *a* fluorescence, and rate of photosynthesis were measured in each replica. Results were reported as mean values ± standard deviation (SD).

2.2 Determination of the number of cells

The flow cytometry was used to establish the initial number of picocyanobacteria cells and to measure the final cells concentration after the incubation period. The number of cells (N) in cultures was counted with flow cytometer BD Accuri™ C6 Plus (BD Biosciences, San Jose, CA, USA) according to the procedure proposed by Śliwińska-Wilczewska et al. (2018b). Events were recorded in list form. Samples were run at a flow rate of approximately 14 μL min^{-1}. Selection of this flow rate was based on previous introductory experiments to determine the most relevant effectiveness. Choosing an adequate discriminator and thresholds plays a key role in recording the cells correctly. The most reasonable solution to record chlorophyll fluorescing cyanobacteria and microalgae is to choose the red fluorescence as the discriminator (Fig. S1) and to select a high threshold, high enough to eliminate optical and electronic noise (Marie et al., 2005). Concerning this, the discriminator was set on the red (chlorophyll) fluorescence with a standard threshold of 80,000 on FSC-H. Flow was daily calibrated with Spherotech 6- and 8- Peak Validation Beads (BD, San Jose, USA). This ensures that the cytometer works properly and is accurately calibrated for running experiments. Fluorescein isothiocyanate (FITC), phycoerythrin (PE), and PE-Cy5 detectors were daily calibrated with SPHERO™ Rainbow Calibration Particles (BD, San Jose, USA), and the Allophycocyanin (APC) channel was calibrated with SPHERO 6-peaks Allophycocyanin Calibration Particles. Detectors FL1, FL2, and FL3 read fluorescence emissions excited by the blue laser (480 nm), while detector FL4 reads emissions excited by the red laser (640 nm).

2.3 Determination of the pigments content

The concentration of photosynthetic pigments of analyzed picocyanobacteria was measured by the spectrophotometric method (Strickland and Parsons, 1972). The analysis of mL-specific (pigment content per mL) and cell-specific (pigment content per cell) pigmentation was conducted. Note that mL-specific means volume-specific, whereas the volume is fixed to 1 mL. After seven days of incubation, 4 mL of culture was filtered in order to separate the picocyanobacteria cells from the medium. Chl *a* and carotenoids (Car) were extracted from the PCY cells with cold 90% acetone (5 mL). To improve extraction, the cells were disintegrated for two minutes by ultrasonication. Then, the test-tube with the extract was held in the dark for three hours at -60°C. To remove cell debris and filter out the particles, the extracts were centrifuged at 10,000 rpm (8496 × g) for 5 min (Sigma 2-16P, Osterode am Harz, Germany). The absorbance of pigments was estimated on the basis of Beckman spectrophotometer UV-VIS DU 530 measurements at specific wavelengths (750, 665 and 480 nm), using 1 cm quartz cuvette. Pigment concentration was calculated according to Strickland and Parsons (1972). The following formulas have been used: Chl *a* ($\mu g\ mL^{-1}$) = $11.236(A_{665}-A_{750})V_a/V_b$, Car ($\mu g\ mL^{-1}$) = $4(A_{480}-A_{750})V_a/V_b$, where: V_a - extract volume (in this study 5 mL), V_b - sample volume (in this study 4 mL), and A_x - absorbance estimated at wavelength x in a 1-cm cuvette.

2.4 Chlorophyll fluorescence analyses

Chl *a* fluorescence was measured with a Pulse Amplitude Modulation (PAM) fluorometer (FMS1, Hansatech, King's Lynn, Norfolk, UK). The FMS1 uses a 594 nm amber modulating beam with 4-step frequency control as a measuring light and is equipped with a dual-purpose halogen light source providing actinic light (0 – 3000 µmol photons m^{-2} s^{-1} in 50 steps) and a saturating pulse (0 – 20000 µmol photons m^{-2} s^{-1} in 100 steps). FMS1 also has a 735 nm far-red LED source for preferential PSI excitation allowing accurate determination of the F_o' parameter. Samples were filtered onto 13-mm glass fiber filters (Whatman GF/C, pore size = 1.2 µm). Before measurement, the filtered sample was kept in the dark for 10 min. The maximum photochemical efficiency of photosystem II (PSII) at dark-adapted state (F_v/F_m) and the photochemical efficiency of PSII under actinic light intensity (ΦPSII) were estimated. The actinic light was different for cultures grown in different environmental conditions and referred to the PAR value in respective scenarios. The above is similar to the method used by Campbell et al. (1998).

2.5 Measurements of photosynthesis rate

The measurements of oxygen evolution were carried out on the seventh day of the experiment using a Clark-type oxygen electrode (Chlorolab 2, Hansatech). Temperature was controlled with a cooling system LAUDA (E100, Germany). Illumination was provided by a high intensity probe-type light array with 11 red LED's centered on 650 nm. Irradiance was measured with a quantum sensor (Quantitherm, Hansatech, King's Lynn, Norfolk, UK). Dark respiration was estimated from O_2 uptake by cells incubated in the dark. Experimental data (photosynthetic parameters, i.e., the photosynthetic capacity (P_m), the initial slope of *P-E* curve (α) and the dark respiration (R_d)) was fitted to the photosynthetesis irradiance response (*P-E*) curves using equation (Jassby and Platt, 1976) and Statistica® 13.1 software (Sakshaug et al., 1997).

2.6 Statistical analyses

The effect of light and temperature separately and then their combinations impact on growth, pigments content, fluorescence and photosynthesis performance of examined strains were analyzed using two-way variance analysis (ANOVA). A post hoc test (Tukey's HSD) was used to show which results differed under varied conditions over the experimental period (Sheskin 2000). The confident levels in the statistical analysis were: 95% (*$p < 0.05$), 99% (**$p < 0.01$), 99.9% (***$p < 0.001$). The statistical analyses were performed using Statistica® 13.1 and Matlab 2012b software. According to the literature, light and temperature are major factors controlling the growth and distribution of picocyanobacteria (e.g.: Jasser and Arvola, 2003), and they may have considerable significance on the abundance of the *Synechococcus* community (Glover, 1985; Glover et al., 1985; 1986, Joint and Pomroy, 1986; Jasser and Arvola, 2003; Jasser, 2006; Jodłowska and Śliwińska, 2014). Due to that, it was decided that light and temperature would be the independent variables in ANOVA and post-hoc test analysis. The dependent variable was always the parameter, which had been measured.

3 Results

3.1 Number of cells

For all three picoplankton strains, ANOVA analysis indicated that in each scenario the independent variable (temperature or PAR) significantly influenced the dependent variable. What is more, post-hoc tests indicated that multiple factors (T and PAR together) had an impact on the PCY growth.

According to post-hoc tests, 2008 multiple comparisons (70%) out of all 2880 completed for three strains, indicated the highest statistical significance (Tukey HSD, *** $p < 0.001$), 160 multiple comparisons (6%) pointed to the statistical significance of 0.001 < ** $p < 0.01$, and 114 (4%) showed the significance of 0.01 < * $p < 0.05$. The rest of the multiple comparisons (598, 20%) indicated no statistically significance differences (Tukey HSD, $p \geq 0.05$).

Both PAR and T affected the number of *Synechococcus* sp. BA-120 cells significantly *(ANOVA, $F_{9,32} = 42.3$, *** $p < 0.001$, ANOVA, $F_{9,32} = 22.7$, *** $p < 0.001$, ANOVA, $F_{9,32} = 9.6$, *** $p < 0.001$ and ANOVA, $F_{9,32} = 12.2$, *** $p < 0.001$, for salinity 3, 8, 13, 18 PSU, respectively)*. For BA-120, the number of cells increased with T in each medium (salinities 3, 8, 13, 18 PSU) (Fig. 1A, a-d). The minimum number of cells was estimated in salinity 3 PSU, T 10°C and PAR 10 μmol photons m^{-2} s^{-1} (1.6×10^6 cell mL^{-1}, Fig. 1A, a), whilst the maximum in salinity 18 PSU, T 25°C, PAR 190 μmol photons m^{-2} s^{-1} (11.5×10^6 cell mL^{-1}, Fig. 1A, d). The decrease in number of cells was observed from PAR 190 μmol photons m^{-2} s^{-1} onwards. This can likely be related to the photo-inhibition of photosystem II (PSII). The above was the case in each salinity (Figs. 1A, a-d). Additionally, the results analysis (Fig 1A, a-d) showed that the most important environmental factor influencing BA-120 number of cells was T, with PAR playing an additional role, for instance in the context of photo-inhibition. This was pronounced the most within lower temperatures (10 and 15°C), where the change in BA-120 abundance along with PAR increase was barely observed being plainly visible along with T increase at once. Multiple comparisons tests pointed to the strong significance of PAR and T combined in influencing the number of *Synechococcus* sp. BA-120 cells. According to the statistics, 82% of multiple comparisons were statistically significant (Tukey HSD, * $p < 0.05$) with 91% of them having the highest significance level (Tukey HSD, *** $p < 0.001$).

Both PAR and T also significantly affected the number of *Synechococcus* sp. BA-124 cells *(ANOVA, $F_{9,32} = 7.9$, *** $p < 0.001$, ANOVA, $F_{9,32} = 13.6$, *** $p < 0.001$, ANOVA, $F_{9,32} = 8.4$, *** $p < 0.001$ and ANOVA, $F_{9,32} = 2.8$, ** $p < 0.01$, for salinity 3, 8, 13, 18 PSU, respectively)*. For BA-124, number of cells increased with T and PAR in all salinities (Figs. 1B, a-d). The lowest number of cells was calculated in salinity 3 PSU, T 10°C and PAR 10 μmol photons m^{-2} s^{-1} (2.0×10^6 cell mL^{-1}, Fig. 1B, a) and the highest number of cells was reached in salinity 18 PSU, T 25°C, PAR 280 μmol photons m^{-2} s^{-1} (43.6×10^6 cell mL^{-1}, Fig. 1B, d). High abundances were estimated also under the highest T and PAR conditions in salinity 13 PSU, where a number of cells equalled 41.1×10^6 cell mL^{-1} (Fig. 1B, c). Generally, the number of cells was the highest in BA-124 cultures when compared to BA-120 and BA-132 cultures in respective scenarios. One of the observations was the difference in BA-124 number of cells between lower and higher PAR and T conditions (scenarios with lower PAR and T and scenarios with higher PAR and T). BA-124 seemed to be more sensitive to changes in PAR and T in their lower rather than in higher ranges. Regarding salinity, the highest number of BA-124 cells were noted in moderate- and high-salinity mediums. Optimum salinities for strain BA-124 were 8 and 13 PSU. Due to post-hoc analysis, salinity 13 PSU differentiated the conditions for cell abundances under different PAR and T at a lower degree when compared to other salinities under respective PAR and T (the least statistically significant differences observed in medium 13 PSU), which is also noticeable in Fig. 1B, c. Another feature of BA-124 was the number of cells in low T and high PAR scenarios were nearly equal to cell abundances in high T and low PAR scenarios. This was not the case for BA-120 and BA-132 strains. The observation was supported by Tukey's tests, where only few statistically significant differences in number of cells were observed between scenarios with elevated PAR (280 μmol photons m^{-2} s^{-1}), low T (10, 15°C) and those with high T (25°C) and low PAR (10 μmol photons m^{-2} s^{-1}). These differences were observed between 15°C and 280 μmol photons m^{-2} s^{-1} and 25°C and 10 μmol photons m^{-2} s^{-1} in salinities 3 and 8 PSU (Tukey HSD, ** $p < 0.05$ in both cases, Figs. 1B, a-b). Multiple comparisons tests showed high significance of combinations of PAR and T in affecting the number of cells. According to Tukey HSD tests, 72% of multiple comparisons were statistically significant (* $p < 0.05$) with 82% of them with the highest significance level (*** $p < 0.001$).

Similarly to BA-120 and BA-124, it was found that PAR and T significantly affected the number of *Synechococcus* sp. BA-132 cells *(ANOVA, $F_{9,32} = 6.8$, *** $p < 0.001$, ANOVA, $F_{9,32} = 5.4$, *** $p < 0.001$, ANOVA, $F_{9,32} = 5.6$, *** $p < 0.001$ and ANOVA, $F_{9,32} = 12.5$, ** $p < 0.01$, for salinity 3, 8, 13, 18 PSU, respectively)*. For BA-132, the positive impact of T and PAR on number of cells (Figs. 1C, a-d) was observed in each medium. Note that positive impact means the increasing (positive) dependency, whilst negative impact means decreasing (negative) dependency between the independent and dependent variable, e.g.: between T and abundance. Salinity played a more significant role here than when compared to BA-124. It was found that the higher the salinity, the higher the number of cells of BA-132. What is more, according to the statistical analysis, salinity 18 PSU differentiated the number of cells the most (Fig. 1C, d). In salinity 18 PSU, the cell abundances could be described as a linear increasing function of ambient T and PAR. This was also observed in other salinities but not as intensively pronounced as in the highest-saline medium. Moreover, in high salinity, the sensitivity of number of cells to T changes was much lower than in low salinities. PAR did not determine the number of cells as strongly as T, which was quite consistent to the observation noted for BA-120. The minimum number of cells was observed in 3 PSU, 10°C and 10 μmol photons m^{-2} s^{-1} (1.4×10^6 cell mL^{-1}, Fig. 1C, a), whilst the maximum in 18 PSU, 25°C, 280 μmol photons m^{-2} s^{-1} (16.1×10^6 cell mL^{-1}, Fig. 1C, d). In addition, the lowest values of BA-132 number of cells were calculated for the lowest T and PAR condition in each salinity. Tukey HSD post hoc tests indicated high significance of the combination of PAR and T in affecting the cell abundances. Regarding those tests, 84% of multiple comparisons were statistically significant (* $p < 0.05$) with 90% of them with the highest significance (*** $p < 0.001$).

Concerning all three strains, high salinity generally had a positive impact on number of *Synechococcus* sp. cells. What is more, the relations between salinity and number of cells for all strains, especially red and brown were almost increasing linearly with the highest average increase for BA-132.

3.2 Pigment content

The results showed that for all strains, cell-specific pigment composition (pigment content per cell) was environmentally driven (Figs. 2, 3). The analysis of mL-specific pigmentation (pigment content per mL) was also done (Figs. S2 and S3 in Supplement), however, the mL-specific pigment content is another way to illustrate the biomass and that is why it is not described in this section in detail.

It was estimated, that PAR and T significantly affected the Chl *a* cell-specific content of *Synechococcus* sp. BA-120 *(ANOVA,* $F_{9,32} = 33.7$, *** $p < 0.001$, *ANOVA,* $F_{9,32} = 5.3$, *** $p < 0.001$, *ANOVA,* $F_{9,32} = 15.6$, *** $p < 0.001$ *and ANOVA,* $F_{9,32} = 5.7$, *** $p < 0.001$, *for salinity 3, 8, 13, 18 PSU, respectively)*. Both PAR and T also affected the Car content in the BA-120 strain cells significantly *(ANOVA,* $F_{9,32} = 25.8$, *** $p < 0.001$, *ANOVA,* $F_{9,32} = 7.5$, *** $p < 0.001$, *ANOVA,* $F_{9,32} = 7.3$, *** $p < 0.001$, *and ANOVA,* $F_{9,32} = 12.0$, *** $p < 0.001$, *for salinity 3, 8, 13, 18 PSU, respectively)*. It was found that cell-specific Chl *a* and Car concentrations decreased with the increase of salinity (Figs. 2A, 3A). On average, the cell content of pigments for BA-120 was the highest when compared to the other strains. Chl *a* concentration dominated over Car concentration in each scenario. What is more, there were very high cell-specific concentrations of Chl *a* observed for the whole T range at low PAR. Maximum Chl *a* content was measured under T 25°C and PAR 10 μmol photons m^{-2} s^{-1}. This was the case in each salinity. The highest Chl *a* concentration within all scenarios was reached in BA-120 cells in salinity 3 PSU and was equal to 0.339 pg $cell^{-1}$ (Fig. 2A, a). For other salinities these maximums were as follows: 0.233 pg $cell^{-1}$ (8 PSU, Fig. 2A, b), 0.164 pg $cell^{-1}$ (13 PSU, Fig. 2A, c), 0.100 pg $cell^{-1}$ (18 PSU, Fig. 2A, d). The highest Car content was measured in salinity 3 PSU under T of 20°C and PAR 10 μmol photons m^{-2} s^{-1} and reached 0.160 pg $cell^{-1}$ (Fig. 3A, a). The lowest concentrations of Chl *a* (0.038 pg $cell^{-1}$) and Car (0.031 pg $cell^{-1}$) were measured in salinity 18 PSU, T 25°C, PAR 190 μmol photons m^{-2} s^{-1} (Fig. 2A, d) and salinity 18 PSU, T 15°C, PAR 280 μmol photons m^{-2} s^{-1} (Fig. 3A, d), respectively. Multiple comparisons tests indicated the significance of PAR and T combined in shaping the pigmentation. Due to those tests, 52% and 55% of multiple comparisons in Chl *a* and Car content analysis, respectively, were statistically significant (Tukey HSD, * $p < 0.05$) with 80% (for Chl *a*) and 74% (for Car) of them with the highest significance (Tukey HSD, *** $p < 0.001$).

Both PAR and T affected the Chl *a* cell-specific content *(ANOVA,* $F_{9,32} = 3.3$, ** $p < 0.01$, *ANOVA,* $F_{9,32} = 8.3$, *** $p < 0.001$, *ANOVA,* $F_{9,32} = 69.8$, *** $p < 0.001$ *and ANOVA,* $F_{9,32} = 17.5$, *** $p < 0.001$, *for salinity 3, 8, 13, 18 PSU, respectively)* and Car cell-specific content *(ANOVA,* $F_{9,32} = 4.6$, *** $p < 0.001$, *ANOVA,* $F_{9,32} = 65.5$, *** $p < 0.001$, *ANOVA, $F_{9,32}$ = 83.1, *** $p < 0.001$ and ANOVA, $F_{9,32}$ = 43.2, *** $p < 0.001$, for salinity 3, 8, 13, 18 PSU, respectively)* of *Synechococcus* sp. BA-124 significantly. Generally, PAR and high T increase had a negative impact on pigmentation (Figs. 2B, 3B). Maximum values of cell-specific Chl *a* and Car concentrations were measured under 10°C and 10 μmol photons m^{-2} s^{-1} in each salinity medium. These values, concerning salinities from the lowest to the highest, were as follows: 0.095, 0.102. 0.176, 0.148 pg $cell^{-1}$ for Chl *a* (Figs. 2B, a-d) and 0.051, 0.067, 0.087, 0.079 pg $cell^{-1}$ for Car (Figs. 3B, a-d). Nonetheless, there were also some exceptions. In salinity 3 PSU, high Car contents were calculated under 280 μmol photons m^{-2} s^{-1} and T: 15, 20°C and equaled to 0.042 pg $cell^{-1}$ and 0.041 pg $cell^{-1}$, respectively (Fig. 3B, a). On average, salinity increase had a negative impact on pigmentation. The lowest cell-specific concentrations of Chl *a* and Car in BA-124 cells were estimated in the same scenario: salinity 18 PSU, T 10°C, PAR 280 μmol photons m^{-2} s^{-1} and were equal to 0.013 pg $cell^{-1}$ (Fig. 2B, d) and 0.009 pg $cell^{-1}$ (Fig. 3B, d), for Chl *a* and Car, respectively. Multiple comparisons tests pointed to the significance of PAR and T combined in influencing the pigmentation. According to the statistics, 47% and 54% of multiple comparisons in Chl *a* and Car content analysis, were statistically significant (Tukey HSD, * $p < 0.05$) with 83% (for Chl *a*) and 79% (for Car) of them with the highest significance level (Tukey HSD, *** $p < 0.001$).

It was also examined that PAR and T affected the Chl *a* cell-specific content *(ANOVA, $F_{9,32}$ = 6.5, $p < 0.001$, ANOVA, $F_{9,32}$ = 11.1, $p < 0.001$, ANOVA, $F_{9,32}$ = 21.5, $p < 0.001$ and ANOVA, $F_{9,32}$ = 6.5, $p < 0.001$, for salinity 3, 8, 13, 18 PSU, respectively)* and Car cell-specific content *(ANOVA, $F_{9,32}$ = 8.6, $p < 0.001$, ANOVA, $F_{9,32}$ = 9.6, $p < 0.001$, ANOVA, $F_{9,32}$ = 4.6, $p < 0.001$ and ANOVA, $F_{9,32}$ = 26.8, $p < 0.001$, for salinity 3, 8, 13, 18 PSU, respectively)* of *Synechococcus* sp. BA-132 significantly. It was found that salinity increase had a negative impact on cell-specific Chl *a* and Car concentrations. BA-132 was richer in cell-specific pigments than BA-124 (Figs. 2C, 3C). Along with PAR increase, the Chl *a* concentration decreased significantly. The maximum Chl *a* cell-specific content was measured in moderate or high T (20°C in salinity 13 PSU and 25°C in salinity 3, 8, 18 PSU) under the lowest PAR (10 μmol photons m^{-2} s^{-1}). These maximums were 0.299 pg $cell^{-1}$ in salinity 3 PSU (Fig. 2C, a), 0.248 pg $cell^{-1}$ in salinity 8 PSU (Fig. 2C, b), 0.151 pg $cell^{-1}$ in salinity 13 PSU (Fig. 2C, c) and 0.073 pg $cell^{-1}$ in salinity 18 PSU (Fig. 2C, d). Consistently with Chl *a*, Car cell-specific content maximums were also measured under the lowest PAR (10 μmol photons m^{-2} s^{-1}) but contrary to Chl *a*, at the lowest T (10°C). These maximums were: 0.194 pg $cell^{-1}$ in salinity 3 PSU (Fig. 3C, a), 0.131 pg $cell^{-1}$ in salinity 8 PSU (Fig. 3C, b), 0.097 pg $cell^{-1}$ in salinity 13 PSU (Fig. 3C, c), 0.062 pg $cell^{-1}$ in salinity 18 PSU (Fig. 3C, d). Minimums of Chl *a* and Car cell-specific contents within all scenarios were estimated in salinity 18 PSU, T 15°C and PAR 280 μmol photons m^{-2} s^{-1} being equal to 0.020 pg $cell^{-1}$ (Fig. 2C, d) and 0.19 pg $cell^{-1}$ (Fig. 3C, d), for Chl *a* and Car, respectively. Regarding Chl *a* for minimum content per cell the same concentration as above mentioned (0.020 pg $cell^{-1}$) was also estimated in salinity 13 PSU for the same conditions of T and PAR (Fig. 2C, c). Tukey HSD tests pointed to the significance of PAR and T combined in impacting the pigmentation. According to those tests, 66% and 61% of multiple comparisons in Chl *a* and Car content analysis, respectively, were statistically significant (Tukey HSD, * $p < 0.05$), with 81% (for Chl *a*) and 75% (for Car) of them with the highest significance (Tukey HSD, *** $p < 0.001$).

3.3 Chl *a* fluorescence

The parameters of Chl *a* fluorescence were depicted as two-factor-dependent graphs, where the values in between the specific measurements were interpolated (Figs. 4, 5). For all strains, Chl *a* fluorescence parameters were measured and examined. These parameters were: the maximum photochemical efficiency of photosystem II (PSII) at dark-adapted state (F_v/F_m) and the photochemical efficiency of PSII under actinic light intensity (ΦPSII).

The results showed that PAR and T affected F_v/F_m *(ANOVA, $F_{9,32}$ = 5.2, $p < 0.001$, ANOVA, $F_{9,32}$ = 5.7, $p < 0.001$, ANOVA, $F_{9,32}$ = 4.8, $p < 0.001$ and ANOVA, $F_{9,32}$ = 33.9, $p < 0.001$, for salinity 3, 8, 13, 18 PSU, respectively)* and ΦPSII *(ANOVA, $F_{9,32}$ = 4.5, $p < 0.001$, ANOVA, $F_{9,32}$ = 5.7, $p < 0.001$, ANOVA, $F_{9,32}$ = 6.3, $p < 0.001$ and ANOVA, $F_{9,32}$ = 2.3, $p < 0.05$, for salinity 3, 8, 13, 18 PSU, respectively)* of *Synechococcus* sp. BA-120 significantly. For this strain, especially in low

T scenarios and in all scenarios with the lowest salinity, higher F_v/F_m was observed for 280 μmol photons m^{-2} s^{-1} when compared to 190 μmol photons m^{-2} s^{-1} (Fig. 4A, a). Generally, strong fluctuations were noticeable in F_v/F_m values, which disabled the fixed environmentally driven pattern determination. However, there was a constant relation noted between T and PAR and ΦPSII. PAR and T increase had a negative impact on ΦPSII. The impact was the strongest in low salinity (Figs. 5A, a-b). Nonetheless, in each salinity, the lowest ΦPSII were observed under the highest T and elevated PAR (190 or 280 μmol photons m^{-2} s^{-1}). On the contrary, the highest ΦPSII values were calculated in the lowest T and PAR conditions in every salinity. The highest F_v/F_m, for all BA-120 experiments equaled 0.804 and was estimated for scenario: salinity 18 PSU, T 10°C, PAR 280 μmol photons m^{-2} s^{-1} (Fig. 4A, d). Generally, maximum values of F_v/F_m in each medium were associated with the lowest temperature. Minimum F_v/F_m within all scenarios was estimated for salinity 3 PSU, T 25°C and PAR 190 μmol photons m^{-2} s^{-1} (0.409, Fig. 4A, a). Concerning ΦPSII, the greatest value was 0.768 estimated in salinity 18 PSU, T 10°C and PAR 10 μmol photons m^{-2} s^{-1} (Fig. 5A, d). Minimum ΦPSII was measured in salinity 3 PSU, T 25°C and PAR 280 μmol photons m^{-2} s^{-1} (0.241, Fig. 5A, a). Multiple comparisons tests pointed to a strong environmental influence on Chl *a* fluorescence parameters. Regarding F_v/F_m, 65% of all comparisons were statistically significant (Tukey HSD, * $p < 0.05$) with 78% of them having the highest significance (Tukey, HSD, *** $p < 0.001$). For ΦPSII the percentages were as follows: 80% of all comparisons were statistically significant (Tukey HSD, * $p < 0.05$) and 87% of them had the highest significance (*** $p < 0.001$).

Both PAR and T significantly affected F_v/F_m *(ANOVA, $F_{9,32} = 46.2$, *** $p < 0.001$, ANOVA, $F_{9,32} = 5.1$, *** $p < 0.001$, ANOVA, $F_{9,32} = 5.0$, *** $p < 0.001$ and ANOVA, $F_{9,32} = 20.6$, *** $p < 0.001$, for 3, 8, 13, 18 PSU, respectively)* and ΦPSII *(ANOVA, $F_{9,32} = 25.0$, *** $p < 0.001$, ANOVA, $F_{9,32} = 11.6$, *** $p < 0.001$, ANOVA, $F_{9,32} = 15.4$, $p < 0.001$ and ANOVA, $F_{9,32} = 5.2$, $p < 0.001$, for 3, 8, 13, 18 PSU, respectively)* of *Synechococcus* sp. BA-124. For this strain, F_v/F_m reached the lowest values when compared to the respective incubations of other strains. The values of F_v/F_m generally decreased along with PAR and T increases but with some exceptions. Generally, ΦPSII environmentally driven characteristics were similar to F_v/F_m characteristics. The F_v/F_m minimums were measured under the lowest T and highest PAR in each salinity (Figs. 4B, a-d). The lowest value within all scenarios was 0.124 and was observed in salinity 3 PSU, T 10°C and PAR 280 μmol photons m^{-2} s^{-1} (Fig. 4B, a). The F_v/F_m maximums were estimated for the highest T and the lowest PAR in each salinity. The highest F_v/F_m equaled 0.560 for salinity 3 PSU, T 25°C and PAR 10 μmol photons m^{-2} s^{-1} (Fig. 4B, a). Minimums of ΦPSII, consistently with F_v/F_m, were noted under the lowest T and highest PAR. The lowest ΦPSII within all BA-124 experiments was 0.114 (followed by the minimum in salinity 3 PSU being equal to 0.116, Fig. 5B, a) and was measured in salinity 13 PSU (Fig. 5B, c). Maximums of ΦPSII were observed in the highest T and lowest PAR in each medium, similarly to F_v/F_m. The greatest value of ΦPSII was 0.542 and was measured in salinity 3 PSU, T 25°C and PAR 10 μmol photons m^{-2} s^{-1} (Fig. 5B, a). Tukey HSD post hoc test showed that PAR and T combined influenced Chl *a* fluorescence parameters significantly. Concerning F_v/F_m, 77% of all comparisons were statistically significant (* $p < 0.05$) with 88% of them having the highest significance (*** $p < 0.001$). For ΦPSII the percentages were as follows: 79% of all comparisons were statistically significant (* $p < 0.05$) and 89% of them had the highest significance (*** $p < 0.001$).

It was found that both PAR and T affected F_v/F_m *(ANOVA, $F_{9,32} = 4.3$, $p < 0.001$, ANOVA, $F_{9,32} = 4.8$, $p < 0.001$, ANOVA, $F_{9,32} = 4.5$, $p < 0.001$ and ANOVA, $F_{9,32} = 5.7$, $p < 0.001$, for salinity 3, 8, 13, 18 PSU, respectively)* and ΦPSII *(ANOVA, $F_{9,32} = 10.1$, $p < 0.001$, ANOVA, $F_{9,32} = 7.7$, $p < 0.001$, ANOVA, $F_{9,32} = 4.7$, $p < 0.001$ and ANOVA, $F_{9,32} = 7.0$, $p < 0.001$, for salinity 3, 8, 13, 18 PSU, respectively)* of *Synechococcus* sp. BA-132, significantly. For this strain, F_v/F_m decreased along with the PAR increase but was positively affected by T in each salinity (Figs. 4C, a-d). Minimum values of F_v/F_m were measured in the highest PAR and the lowest T in each salinity. The lowest F_v/F_m within all experiments on BA-132 was estimated in salinity 13 PSU (F_v/F_m = 0.155, Fig. 4C, c). In salinity 3 PSU, under aforementioned conditions of T and PAR, the F_v/F_m value was also low compared to the others and equaled 0.160 (Fig. 4C, a). The maximums of F_v/F_m were measured in T 25°C and PAR 10 μmol photons m^{-2} s^{-1}. This was the case for all mediums. The highest F_v/F_m were noted in salinities 13 and 18 PSU and equaled 0.742 (Fig. 4C, c) and 0.733 (Fig. 4C, d), respectively. The lowest ΦPSII were noted under the highest PAR and T conditions in every salinity (Figs. 5C, a-d). The minimum ΦPSII, within all gathered results, was obtained in salinity 3 PSU and equaled 0.281 (Fig. 5C, a). Maximums of ΦPSII were measured under completely opposite conditions to the ones stating for minimums, i.e. the lowest PAR and T. The highest ΦPSII, 0.786, was noted in salinity 8 PSU, T 10°C and PAR 10 μmol photons $m^{-2} s^{-1}$ (Fig. 5C, b). The ΦPSII reached generally higher values than F_v/F_m in BA-132 experiments. ΦPSII reached lower values than ΦPSII measured under respective conditions for two other strains. Multiple comparisons tests point to a strong environmental influence on Chl *a* fluorescence parameters. For F_v/F_m, 78% of all comparisons were statistically significant (Tukey HSD, * $p < 0.05$) with 89% of them with the highest significance (Tukey, HSD, *** $p < 0.001$). For ΦPSII, 82% of all comparisons were statistically significant (Tukey HSD, * $p < 0.05$), with 89% of them having the highest significance level (Tukey, HSD, *** $p < 0.001$).

Generally, for the BA-120 strain, F_v/F_m was affected negatively by T increase, while BA-124 and BA-132 strains were affected positively. T increase had a positive impact on ΦPSII for BA-124 and a negative impact for BA-120 and BA-132. On average, ΦPSII decreased along with PAR increase in all cultures.

3.4 Photosynthesis

Net photosynthetic light-response curves for three PCY strains were analyzed. For all cultures, the photosynthesis parameters were: maximum of photosynthesis, photosynthesis efficiency at low irradiance, and dark respiration (P_m, α, R_d, respectively) and these were estimated for Chl *a*-specific and cell-specific domains (Figs. S4-S6 in Supplement). It should be noted that dark respiration values were negative (less oxygen than carbon dioxide (CO_2)), which meant the lower R_d, the less net oxygen concentration was. This, in turn, indicated higher respiration rate.

For BA-120 statistical study showed significant dependence of PAR and T on Chl *a*-specific P_m in salinities 3, 8 and 18 PSU *(ANOVA, $F_{9,32} = 2.4$, $p < 0.05$, $F_{9,32} = 3.2$, $p < 0.05$ and $F_{9,32} = 5.2$, $p < 0.001$, respectively)* and pointed to no statistically significant dependence of ecological conditions on P_m in salinity 13 PSU *(ANOVA, $p \geq 0.05$)*. Regarding cell-specific P_m there was no statistically significant influence of PAR and T on this parameter in salinity 18 PSU *(ANOVA, $p \geq 0.05$)* but was in salinity 3 PSU *(ANOVA, $F_{9,32} = 3.5$, $p < 0.05$)*, 8 PSU *(ANOVA, $F_{9,32} = 2.6$, $p < 0.05$)*, and 13 PSU *(ANOVA, $F_{9,32} = 3.0$, $p < 0.05$)*. For Chl *a*-specific α, statistical study indicated no environmental impacts in salinities 3, 8 and 13 PSU but an impact of PAR and T in salinity 18 PSU *(ANOVA, $F_{9,32} = 2.7$, $p < 0.05$)*, while for cell-specific α statistical significance of PAR and T influence was obtained for all salinities *(ANOVA, $F_{9,32} = 5.1$, $p < 0.001$, ANOVA, $F_{9,32} = 2.9$, $p < 0.05$, ANOVA, $F_{9,32} = 2.5$, $p < 0.05$ and ANOVA, $F_{9,32} = 4.8$, $p < 0.001$, for salinity 3, 8, 13 and 18 PSU, respectively)*. Regarding R_d, two-way ANOVA pointed to no environmental determination of Chl *a*-specific R_d values *(ANOVA, $p > 0.05$)* but it showed the influence of PAR and T on cell-specific R_d *(ANOVA, $F_{9,32} = 9.2$, $p < 0.001$, ANOVA, $F_{9,32} = 3.8$, $p < 0.01$, ANOVA, $F_{9,32} = 3.8$, $p < 0.01$, ANOVA, $F_{9,32} = 4.5$, $p < 0.001$, in salinities 3, 8, 13, 18 PSU, respectively)*. Tukey HSD tests pointed to some statistically significant multiple comparisons but showed a weak influence of PAR and T combined on Chl *a*-specific parameters. Regarding α, only 3% of all multiple comparisons were statistically significant (* $p < 0.05$) with 7% of them at the highest statistical significance level (*** $p < 0.001$). For P_m, 36% of all multiple comparisons were statistically significant (* $p < 0.05$) with 64% of them with the highest significance (*** $p < 0.001$). Regarding R_d, as mentioned above, no statistically significant analysis of variance was indicated. Due to that, no post hoc tests were proceeded. Note that in order to shorten the text and emphasize reading, in this section the notation for the percentage of all statistically significant multiple comparisons (* $p < 0.05$) and the percentage of the multiple comparisons of the highest significance within the all significant comparisons (*** $p < 0.001 \times$ (* $p < 0.05)^{-1}$) were written in parenthesis, one by one, separated with comma. For instance: X (15%, 20%) would mean that there were 15% of statistically significant multiple comparisons for parameter X in the post hoc tests results, whereas 20% of them were statistically the most significant. Similarly to Chl *a*-specific calculations, Tukey HSD test pointed to a selective influence of PAR and T combined on cell-specific parameters. However, this dependence was stronger when compared to Chl *a*-specific estimations (P_m (16%, 52%), α (19%, 43%), R_d (28%, 56%)). Nonetheless, there were also some fixed relations noted for both calculation domains. For Chl *a*-specific photosynthesis, P_m increased along with PAR up to PAR of 190 μmol photons m^{-2} s^{-1} (Figs. S4, a, c). Above this level P_m value started to decrease slightly. This was the case in all salinities. Minimum P_m was measured for cells grown in scenario: salinity 3 PSU, T 15°C, PAR 10 μmol photons m^{-2} s^{-1} and it was 0.12 μmol O_2 (μg Chl *a*)$^{-1}$ h^{-1} (Fig. S4, a), whilst the maximum equalled 1.31 μmol O_2 (μg Chl *a*)$^{-1}$ h^{-1} and was reached in salinity 18 PSU, T 25°C, 190 μmol photons m^{-2} s^{-1} (Fig. S4, c). Dark respiration rate (R_d) increased with T increase and decreased with PAR increase (Figs. S5, a, c). Minimum R_d (-0.31 μmol O_2 (μg Chl *a*)$^{-1}$ h^{-1}) was measured in salinity 18 PSU, T 10°C, PAR 280 μmol photons m^{-2} s^{-1} (Fig. S5, c), while maximum (-0.02 μmol O_2 (μg Chl *a*)$^{-1}$ h^{-1}) was estimated in salinity 3 PSU, T 25°C, PAR 10 μmol photons m^{-2} s^{-1} (Fig. S5, a). On the contrary, it was more difficult to determine a fixed pattern of α changes unequivocally. The most fixed tendency of α changes was observed between all temperature-differenced scenarios in 18 PSU salinity medium (Figs. S6, a, c). Under those conditions, it was noticeable that α decreased with PAR and T increase till it reached PAR level of 190 μmol photons m^{-2} s^{-1}. Then, α started to rise slowly. Regarding all gathered results (all mediums together), minimum α was measured in salinity 3 PSU, T 25°C, PAR 10 μmol photons m^{-2} s^{-1} and equalled 0.002 μmol O_2 (μg Chl *a*)$^{-1}$ h^{-1} [μmol photons m^{-2} s^{-1}]$^{-1}$ (Fig. S6, a), whilst maximum was 0.013 μmol O_2 (μg Chl *a*)$^{-1}$ h^{-1} [μmol photons m^{-2} s^{-1}]$^{-1}$ in salinity 13 PSU, T 10°C, PAR 10 μmol photons m^{-2} s^{-1}. On the other hand, for cell-specific domain, P_m increased along with T and it was more pronounced in higher salinities. Concerning all results, minimum P_m was 28.58 μmol O_2 cell 10^{-9} h^{-1} and, similarly to Chl *a*-specific P_m was measured in scenario: salinity 13 PSU, T 10°C, PAR 10 μmol photons m^{-2} s^{-1}, whilst maximum P_m equalled 55.16 μmol O_2 cell 10^{-9} h^{-1} and was reached in salinity 8 PSU, T 25°C, 190 μmol photons m^{-2} s^{-1} (data not shown). Regarding α, this parameter was generally negatively affected by PAR and T up to PAR of 190 μmol photons m^{-2} s^{-1}. However minimum value was obtained for cells growing in moderate T (salinity 8 PSU, T 20°C, PAR 10 μmol photons m^{-2} s^{-1}) and equalled 0.81 μmol O_2 cell 10^{-9} h^{-1} [μmol photons m^{-2} s^{-1}]$^{-1}$. Maximum α equalled 1.57 μmol O_2 cell 10^{-9} h^{-1} [μmol photons m^{-2} s^{-1}]$^{-1}$ and was measured in salinity 18 PSU, T 10°C, PAR 10 μmol photons m^{-2} s^{-1} (Fig. S6, d). Generally, T and PAR had a positive impact on R_d for cultures grown in PAR range up to 190 μmol photons m^{-2} s^{-1}. For cultures grown under elevated PAR conditions, R_d was lower (more intensive respiration) when compared to low PAR scenarios. The lowest R_d within all BA-120 experiments results was -16.97 μmol O_2 cell 10^{-9} h^{-1} and noted in salinity 3 PSU, T 10°C, PAR 10 μmol photons m^{-2} s^{-1} (Fig. S5, b), whilst the highest R_d was measured in salinity 18 PSU, T 25°C, PAR 100 μmol photons m^{-2} s^{-1} and equalled -2.06 μmol O_2 cell 10^{-9} h^{-1} (Fig. S5, d).

For BA-124, statistical study showed significant dependence of ecological conditions on photosynthesis parameters, excluding Chl *a*-specific α *(ANOVA, $p \geq 0.05$)* and cell-specific P_m *(ANOVA, $p \geq 0.05$)*. For the rest parameters ANOVA results were as follows: Chl *a*-specific P_m *(ANOVA, $F_{9,32} = 4.8$, $p < 0.001$, ANOVA, $F_{9,32} = 19.7$, $p < 0.001$, ANOVA, $F_{9,32} = 9.14$, $p < 0.001$, ANOVA, $F_{9,32} = 6.5$, $p < 0.001$ in salinity 3, 8, 13, 18 PSU, respectively)*; cell-specific P_m *(ANOVA, $F_{9,32} = 7.5$, $p < 0.001$, ANOVA, $F_{9,32} = 6.1$, $p < 0.001$, ANOVA, $F_{9,32} = 4.3$, $p < 0.001$ in salinity 8, 13 and 18 PSU, respectively)*; Chl *a*-specific α *(ANOVA, $F_{9,32} = 5.0$, $p < 0.001$, ANOVA, $F_{9,32} = 3.3$, $p < 0.01$, ANOVA, $F_{9,32} = 3.8$, $p < 0.01$ in salinity 3, 8 and 18 PSU, respectively)*; cell-specific α *(ANOVA, $F_{9,32} = 6.6$, $p < 0.001$, ANOVA, $F_{9,32} = 17.9$, $p < 0.001$, ANOVA, $F_{9,32} = 18.9$, $p < 0.001$, ANOVA, $F_{9,32} = 3.1$, $p < 0.01$, in salinity 3, 8, 13, 18 PSU, respectively)*; Chl *a*-specific R_d *(ANOVA, $F_{9,32} = 10.0$, $p < 0.001$, ANOVA, $F_{9,32} = 4.9$, $p < 0.001$, ANOVA, $F_{9,32} = 3.8$, $p < 0.01$, ANOVA, $F_{9,32} = 2.6$, $p < 0.05$, in salinity 3, 8, 13, 18 PSU, respectively)*; cell-specific R_d *(ANOVA, $F_{9,32} = 13.0$, $p < 0.001$, ANOVA, $F_{9,32} = 2.2$, $p < 0.05$, ANOVA, $F_{9,32} = 40.4$, $p < 0.001$, ANOVA, $F_{9,32} = 3.1$, $p < 0.01$)*. Post-hoc tests showed there must have been other factors, which affected the whole process of photosynthesis as there were many not statistically significant multiple comparisons defined. Generally, Tukey HSD tests pointed to only few statistically significant multiple comparisons, in both Chl *a*-specific, especially for P_m, (P_m (60%, 76%), α (9%, 29%), R_d (30%, 47%) and cell-specific (P_m (22%, 56%), α (34%, 63%), R_d (30%, 74%)) estimations. Nonetheless, for P_m there was a tendency noted, which suggested that on average, the maximum of photosynthesis was higher at elevated PAR. This was the case in both estimations, Chl *a*-specific and cell-specific. Maximum Chl *a*-specific P_m was 3.0 and minimum 0.16 μmol O_2 (μg Chl *a*)$^{-1}$ h^{-1}. These values were measured in salinity 18 PSU in T 25°C, PAR 280 μmol photons m^{-2} s^{-1} and T 10°C, PAR 10 μmol photons m^{-2} s^{-1}, respectively (Fig. S4, g). Maximum cell-specific P_m was obtained in salinity 8 PSU, T 25°C, PAR 280 μmol photons m^{-2} s^{-1} and minimum in salinity 13 PSU, T 20°C, PAR 10 μmol photons m^{-2} s^{-1} (data not shown here). These extreme values were 53.41 and 19.17 μmol O_2 cell·10^{-9} h^{-1}, respectively. It was difficult to determine a fixed relation between ecological state and α changes in both domains, which was supported by the post-hoc test (more than 91% of multiple comparisons were not statistically significant ($p \geq 0.05$) in Chl *a*-specific and more than 35% in cell-specific estimations). Maximum Chl *a*-specific α was 0.02 μmol O_2 (μg Chl *a*)$^{-1}$ h^{-1} [μmol photons m^{-2} s^{-1}]$^{-1}$ and was measured in salinity 3 PSU, T 15°C, PAR 100 μmol photons m^{-2} s^{-1} (Fig. S6, e), while maximum cell-specific α (1.77 μmol O_2 cell 10^{-9} h^{-1} [μmol photons m^{-2} s^{-1}]$^{-1}$) was obtained in salinity 13 PSU, T 10°C, PAR 10 μmol photons m^{-2} s^{-1}. Minimum Chl *a*-specific α was 0.003 μmol O_2 (μg Chl *a*)$^{-1}$ h^{-1} [μmol photons m^{-2} s^{-1}]$^{-1}$ and was measured in two scenarios: salinity 3 PSU, T 10°C, PAR 280 μmol photons m^{-2} s^{-1} (Fig. S6, e) and salinity 18 PSU, T 15°C, PAR 10 μmol photons m^{-2} s^{-1} (Fig. S6, g). Minimum cell-specific α equalled 0.08 μmol O_2 cell 10^{-9} h^{-1} [μmol photons m^{-2} s^{-1}]$^{-1}$ and was measured in salinity 18 PSU, T 15°C, PAR 190 μmol photons m^{-2} s^{-1} (Fig. S6, h). Similarly to α, it was difficult to determine fixed relations between PAR and T and R_d, which was supported by statistics (about 70% of multiple comparisons for both Chl *a*-specific and cell-specific R_d were not statistically significant (Tukey HSD, $p \geq 0.05$)). Nonetheless, it was observed that, generally, R_d decreased along with PAR increase in cell-specific estimations. Maximum Chl *a*-specific and cell-specific R_d was -0.03 μmol O_2 (μg Chl *a*)$^{-1}$ h^{-1} and -1.52 μmol O_2 cell 10^{-9}, respectively. These values were obtained in salinity 13 PSU, T 20°C, PAR 10 μmol photons m^{-2} s^{-1} and salinity 18 PSU, T 20°C, PAR 190 μmol photons m^{-2} s^{-1}, respectively for Chl *a*- and cell-specific calculations. Minimum Chl *a*-specific R_d was measured in salinity 13 PSU, T 10°C, PAR 280 μmol photons m^{-2} s^{-1} and was -0.27 μmol O_2 (μg Chl *a*)$^{-1}$ h^{-1}, whilst minimum cell-specific R_d was measured in salinity 13 PSU, T 10°C, PAR 10 μmol photons m^{-2} s^{-1} and equalled -12.19 μmol O_2 cell 10^{-9} h^{-1} (data not shown here).

For BA-132, statistical study showed significant dependence of PAR and T on Chl *a*- and cell-specific P_m *(for Chl a-specific: ANOVA,* $F_{9,32} = 6.2, p < 0.001$*, ANOVA,* $F_{9,32} = 23.1, p < 0.001$*, ANOVA,* $F_{9,32} = 25.2, p < 0.001$*, ANOVA,* $F_{9,32} = 16.0, p < 0.001$*; for cell-specific: ANOVA,* $F_{9,32} = 4.8, p < 0.001$*, ANOVA,* $F_{9,32} = 24.3, p < 0.001$*, ANOVA,* $F_{9,32} = 24.3, p < 0.001$*, ANOVA,* $F_{9,32} = 21.2, p < 0.001$*; all numbers given for salinities 3, 8, 13, 18 PSU, respectively)*. Regarding other Chl *a*-specific parameters, there were no statistically significant impacts of PAR and T on α in salinities 3, 13, 18 PSU *(ANOVA,* $p \geq 0.05$*)* but were in salinity 8 PSU *(ANOVA,* $F_{9,32} = 2.7, p < 0.05$*)* and no impacts on Chl *a*-specific R_d in salinities 3, 8, 18 PSU *(ANOVA,* $p \geq 0.05$*)* but were in salinity 13 PSU *(ANOVA,* $F_{9,32} = 2.8, p < 0.05$*)*. Regarding other than P_m cell-specific parameters, there was no ecological determination of α noted in salinities 3 and 8 PSU and of R_d in salinity 13 PSU *(ANOVA,* $p \geq 0.05$*),* while there were statistically significant environmental impacts calculated for α in salinity 13 PSU *(ANOVA,* $F_{9,32} = 3.2, p < 0.01$*)* and 18 PSU *(ANOVA,* $F_{9,32} = 2.9, p < 0.05$*)* and for R_d in salinities 3, 8 and 18 PSU *(ANOVA,* $F_{9,32} = 3.2, p < 0.05$*, ANOVA,* $F_{9,32} = 3.1, p < 0.01$*, ANOVA,* $F_{9,32} = 2.4, p < 0.05$*, respectively)*. Tukey HSD tests pointed to statistically significant multiple comparisons, in both Chl *a*-specific and cell-specific maximum of photosynthesis (P_m (68%, 85%), P_m (62%, 76%), respectively). Post hoc tests indicated no significant multiple comparisons for Chl *a*-specific α (>1%, >1%), a few significant multiple comparisons for Chl *a*-specific R_d (8%, 38%), cell-specific α (18%, 67%) and cell-specific R_d (6%, 20%)). It was observed, that in cell-specific estimations, P_m increased along with PAR increase, while α decreased at elevated PAR. It was the most difficult to determine a fixed tendency for the R_d response to changing environmental conditions. This was supported by statistical tests (Tukey HSD, more than 93% of multiple comparisons were not statistically significant ($p \geq 0.05$)). Maximum cell-specific P_m was 158.94 μmol O_2 cell 10^{-9} h^{-1} and was reached in salinity 8 PSU, T 25°C, PAR 280 μmol photons m^{-2} s^{-1}, whilst minimum equalled 28.04 μmol O_2 cell 10^{-9} h^{-1} in salinity 18 PSU, T 15°C, PAR 10 μmol photons m^{-2} s^{-1} (Fig. S4, l). Maximum cell-specific α was 1.78 μmol O_2 cell 10^{-9} h^{-1} [μmol photons m^{-2} s^{-1}]$^{-1}$ and was measured in salinity 13 PSU, T 20°C, PAR 10 μmol photons m^{-2} s^{-1}, while minimum was reached in salinity 18 PSU, T 20°C, PAR 100 μmol photons m^{-2} s^{-1} and equalled 0.19 μmol O_2 cell 10^{-9} h^{-1} [μmol photons m^{-2} s^{-1}]$^{-1}$ (Fig. S6, l). Regarding cell-specific R_d, maximum was measured in salinity 18 PSU, T 15°C, PAR 100 μmol photons m^{-2} s^{-1} and equalled -3.17 μmol O_2 cell 10^{-9} h^{-1} (Fig. S5, l), whilst minimum was -15.55 μmol O_2 cell 10^{-9} h^{-1} and was obtained in salinity 3

PSU, T 10°C, PAR 10 μmol photons $m^{-2}\ s^{-1}$ (Fig. S5, j). For Chl *a*-specific P_m, the increases along with T and salinity was observed, whilst α presented strong changing characteristics between scenarios. The fixed influence of PAR and T on α values was difficult to determine, which was supported by statistics *(ANOVA, $p \geq 0.05$)*. Contrary to the above, it was plainly evident that PAR increase had a negative impact on Chl *a*-specific R_d. Maximum Chl *a*-specific P_m was 6.22 μmol O_2 (μg Chl *a*)$^{-1}$ h^{-1} and was reached in salinity 18 PSU, T 25°C, PAR 280 μmol photons $m^{-2}\ s^{-1}$ (Fig. S4, k), whilst minimum equalled 0.12 μmol O_2 (μg Chl *a*)$^{-1}$ h^{-1} in salinity 3 PSU, T 25°C, PAR 10 μmol photons $m^{-2}\ s^{-1}$ (Fig. S4, i). Maximum Chl *a*-specific α was 0.02 μmol O_2 (μg Chl *a*)$^{-1}$ h^{-1} [μmol photons $m^{-2}\ s^{-1}$]$^{-1}$ and was measured in salinity 18 PSU, T 15°C, PAR 10 μmol photons $m^{-2}\ s^{-1}$ (Fig. S6, k), while minimum was reached in salinity 3 PSU, T 15°C, PAR 10 μmol photons $m^{-2}\ s^{-1}$ and equalled 0.003 μmol O_2 (μg Chl *a*)$^{-1}$ h^{-1} [μmol photons $m^{-2}\ s^{-1}$]$^{-1}$ (Fig. S6, i). Concerning Chl *a*-specific R_d, maximum was measured in salinity 3 PSU, T 20°C, PAR 10 μmol photons $m^{-2}\ s^{-1}$ and equalled -0.02 μmol O_2 cell 10^{-9} h^{-1} (Fig. S5, i), whilst minimum was -0.39 μmol O_2 cell 10^{-9} h^{-1} and was obtained in salinity 13 PSU, T 25°C, PAR 280 μmol photons $m^{-2}\ s^{-1}$. Generally, in both domains, photosynthesis parameters were the highest for BA-132 when compared to other strains.

The analysis of photosynthesis characteristics enabled examining and defining the photoacclimation process of all three strains of *Synechococcus* sp. This was done on the basis of the photosynthetic parameters (Figs. S4-S6) and Photosynthesis-Irradiance (*P-E*) curves (exemplification shown in Fig. 6). The curves were plotted on the basis of laboratory results (Clark oxygen electrode measurements) using the equation of Jassby and Platt (1976). According to a photoacclimation model description (Prezelin, 1981; Prezelin and Sweeney, 1979; Ramus, 1981; Richardson et al., 1983; Pniewski et al., 2016), the results of the present study indicated changes in Photosynthetic Units (PSU) sizes as the photoacclimation mechanism, which occurred most frequently (Table 1). There were also *P-E* curves pointing to some changes in enzymatic reactions and the altering of accessory pigments activity. Changes in PSU numbers were noted as well, but these observations were episodic. In this paper the term 'OTHER' stands for changes in enzymatic reactions and the altering of accessory pigments activity and concerns photoacclimation mechanisms other than changes in PSU sizes (PSUsize) or changes in PSU number (PSUno.). In general, photoacclimation did not occur in low-saline medium (salinity 3). According to the results, photoacclimation mechanisms were observed in only four scenarios with low salinity: BA-120 25°C salinity 3 PSU, BA-124 25°C salinity 3 PSU, BA-132 10°C salinity 3 PSU, and BA-132 25°C salinity 3 PSU. For BA-120, photoacclimation occurred more frequently at higher T (20 and 25°C) than lower T (10 and 15°C). However, if it had been observed in low T conditions, it usually stood for OTHER, not for PSUsize or PSUno. For BA-124 and BA-132 photoacclimation was noted in the whole T range. All photoacclimation mechanisms observed for different strains are listed in Table 1.

4 Discussion

Picoplanktonic organisms show a lot of adaptations, which enable them to spread in aquatic environments (e.g., Stomp et al., 2007; Jodłowska and Śliwińska, 2014; Larsson et al., 2014; Jasser and Callieri, 2017). What is more, picocyanobacteria often dominate and occupy the niches, which are inaccessible for other photoautotrophs. Owing to the fact that PCY are small-sized cells and consequently possess an advantageous surface area to volume ratio, they can assimilate trace amount of nutrients and effectively absorb light. Therefore, in oligotrophic regions of seas and oceans PCY compete with other cyanobacteria and microalgae and it can determine primary production of the whole marine ecosystem (Six et al., 2007a; Richardson and Jackson, 2007; Worden and Wilken, 2016). This is also true for eutrophic basins (Stal et al., 2003; Haverkamp et al., 2008; 2009; Callieri, 2010; Mazur-Marzec et al., 2013).

The distribution of PCY are determined by their optimal ecological requirements for light and temperature. Due to the presented results, PAR and T had positive effects on the number of cells for two out of the three studied strains of *Synechococcus* sp. The highest cell concentrations were noted in scenarios with the highest T (25°C) and the highest PAR level (280 μmol photons $m^{-2}\ s^{-1}$) for BA-124 and BA-132. The BA-120 strain behaved differently when compared to the other strains. For BA-120, the decrease in number of cells was observed in high PAR conditions, i.e. cell abundances for red strain cultures grown under the most elevated PAR were lower than the number of BA-120 cells measured in cultures grown under 190 μmol photons m^{-2} s^{-1}. According to the results derived from pigmentation, Chl *a* fluorescence and photosynthesis sections of the present study, the decrease in number of cells under the elevated PAR could have likely been associated with Photosystem II photo-inhibition. This is a conclusion of a few observations, which are as follows. Firstly, there was a higher cell-specific Car content observed for 280 μmol photons m^{-2} s^{-1} when compared to 190 μmol photons m^{-2} s^{-1}. Secondly, higher F_v/F_m values were observed for 280 μmol photons m^{-2} s^{-1} when compared to 190 μmol photons m^{-2} s^{-1}, especially for low T scenarios and for all scenarios in the lowest salinity medium. Thirdly, for Chl *a*-specific photosynthesis, P_m increased along with PAR until 190 μmol photons m^{-2} s^{-1}, above which the values started to decrease slightly in all salinity mediums. According to the above, a PAR level of 190 μmol photons m^{-2} s^{-1} could be defined as the PSII photo-inhibition point for the red strain. This implies BA-120 did not lead as effective photosynthesis being grown in PAR of more than 190 μmol photons m^{-2} s^{-1} as the cells grown in PAR levels equal or are beneath 190 μmol photons m^{-2} s^{-1}.

Cyanobacteria are generally recognized to prefer low light intensity for growth (Fogg and Thake, 1987; Ibelings, 1996). Some picoplanktonic organisms demonstrated the ability to survive and resume growth after periods of total darkness. Such a pronounced capacity for survival in the dark would enable these organisms to outlive the seasonal rhythm of winter darkness and sinking into the aphotic zone (Antia, 1976). The investigated strains of *Synechococcus* sp. were found to be well adapted to relatively low and high PAR levels. The latter was especially evident at the high treatment T. This conclusion is consistent with the observations of picocyanobacteria maximum abundance at the euphotic zone in coastal and offshore marine waters (Stal et al., 2003; Callieri, 2010). Moreover, Kana and Glibert (1987a,b) showed that *Synechococcus* sp. could grow at irradiance as high as 2000 μmol photon m^{-2} s^{-1}. Regarding the comparison of abundance values of the analyzed strains, the results showed that in all synthetically developed environmental scenarios, BA-124 was the strain of the highest cell abundance. This is consistent with the Baltic Sea field studies (Mazur-Marzec et al., 2013).

Surface and near-surface populations experience extremely variable light and temperature conditions (Millie et al., 1990), and these factors are the ones that affect the composition of photosynthetic pigments and photosynthesis performance of PCY (Jodłowska and Śliwińska, 2014). Picocyanobacteria with a high concentration of PC are chromatically better adapted to harvest longer wavelengths of PAR than those with PE as a dominating pigment. Therefore, such PCY, such as the BA-124 strain, usually dominate in surface euphotic waters (Stal et al., 2003; Haverkamp et al., 2008; 2009). On the other hand, the strains rich in PE (BA-120 and BA-132), usually occurred deeper (Fahnenstiel et al., 1991; Hauschild et al., 1991; Vörös et al., 1991). Nonetheless, generally PCY, thanks to their high concentration of photosynthetic pigments, may occur in waters under low light intensity (Stal et al., 2003). Carotenoids have a dual role in the cell: to maintain a high capacity for photosynthetic light absorption and to provide protection against photooxidation (Siefermann-Harms, 1987). This feature additionally explains why picoplanktonic *Synechococcus* is able to grow successfully both in the surface layer of the sea and also in deeper waters (Stal and Walsby, 2000; Stal et al., 2003). This research showed that regarding BA-120 cell-specific pigments content, there were very high concentrations of Chl *a* observed in the whole T range under low PAR. This could have implied the photoacclimation type, which was the change in PSU number. This mechanism was observed in *P-E* curves for scenario with salinity 8 PSU and temperature 20°C.

PAR and T were the main factors also in terms of influencing the changes in Chl *a* fluorescence in three strains of *Synechococcus* sp. This may likely be linked to a great importance of PCY domination in many aquatic ecosystems during the summer period. Due to Chl *a* fluorescence parameters results, it should be noted that PAR increase always had a negative impact on ΦPSII, which implied that cells, previously acclimated to high light conditions, had lower PSII photosystem efficiency under actinic light.

The results showed that T, PAR and salinity influenced the photosynthesis parameters only to a certain degree. There were many not statistically significant multiple comparisons pointed by post hoc tests. However, it was found that generally, in cell-specific estimations, elevated PAR had a negative effect on α and PAR increase and influenced the respiration negatively. For each of the studied strains of *Synechococcus* sp., the highest α and the lowest R_d were noted for the cells grown under the lowest PAR (10 μmol photons m^{-2} s^{-1}). On the other hand, the highest values of P_m were noted at the highest PAR. It pointed to inability for the cells incubated in low PAR conditions to be as effective in photosynthesis as the cells grown under high irradiances. On the basis of P-E curves derived in this study, three types of photoacclimation mechanisms of *Synechococcus* sp. were observed: change in PSU size, change in PSU number and altering accessory pigments activity and changes in enzymatic reactions. This was a striking observation because in the literature the two first of photoacclimation mechanisms listed above are predominant (Stal et al., 2003; Jodłowska and Śliwińska, 2014). The present study showed that changes in PSU size occur most frequently (Table 1). The second, ranked by frequency of occurrence, was the altering of accessory pigment activity. PSU number changes in *Synechoccocus* sp. occurred rarely, which is consistent with literature (Jodłowska and Śliwińska, 2014). Moreover, in this study, salinity 3 PSU was the medium, where the photoacclimation mechanisms in the *Synechococcus* sp. cells were recognized the least frequently. The changes of photosynthesis parameters (P_m, α, R_d) under different environmental conditions explains the occurrence of different photoacclimation mechanisms. According to the results, *Synechococcus* strains present different ecophysiological characteristics, however, they all demonstrate the tolerance to elevated PAR (for BA-120 to a certain degree) and T levels and could have effectively acclimated to varied water conditions. These strains were able to change the composition of photosynthetic pigments in order to use light quanta better. The ability of *Synechococcus* sp. to sustain its growth in low light conditions and its low photoinhibition in exposure to high light intensities could give PCY an advantage over the other phytoplankton in optically changing waters (Jasser, 2006).

Due to occurrence of extremes in salinity and other environmental conditions in the Baltic Sea area, the Baltic inhabitants are highly adapted to different regions and often reach their physiological limits (Snoeijs-Leijonmalm and Andrén, 2017). The changing environmental conditions the cultures were grown in during the experiments were salinity, T and PAR. Daily mean sea surface temperature (Leppäranta and Myrberg, 2009) presents strongly pronounced annual cycles in the Baltic Sea area. Sea surface temperature (SST) range between about 10 and 20ºC may be timed in the Baltic between June and September with some inter-annual changes (Siegel and Gerth, 2017). SSTs reaching and exceeding 20ºC are also observed in the Baltic basin. For instance, according to Siegel and Gerth (2017), SSTs higher than 20ºC were recorded in almost whole Baltic area beyond Danish Straits, Bothnian Bay and northern Bothnian Basin in the warmest week of 2016, in July. According to above, the temperatures, under which the picocyanobacterium cultures were grown in the present study (10 – 25ºC) can be defined as representative for the Baltic Sea. Furthermore, the salinity ranges applied in the experiment are also Baltic's representatives. The Baltic Sea horizontal salinity gradient is high and different sub-basins are characterized by different mean salinity values. The gradient decreases North towards. The highest salinity is observed in the Baltic Sea boundary to the North Sea (Skagerrak, mean salinity ranges between 28.34 and 32.71), while the lowest mean salinity is observed in the Baltic northernmost regions (around 2.35 – 3.96 in Bothnian Basin). These numbers were determined on the basis of climatological data from the Baltic Atlas of Long-Term Inventory and Climatology (Feistel et al., 2008; 2010). Thus, the presented analysis may derive accurate assumptions regarding the regional distribution of *Synechococcus* sp. strains in the Baltic Sea. For instance, a salinity horizontal gradient can be one of the factors determining the abundance of a certain strain in the basin. More saline waters are most preferred by BA-132. On that basis, one can assume the concentration of this strain will be higher near the Baltic Sea entrance (Danish Straits) than in Bothnian Bay. Additionally, it was observed that despite elevated PAR conditions being more suitable for BA-124 and BA-132 to grow intensively, all analyzed strains were able to survive and grow in low PAR conditions. This is consistent with other previously published Baltic studies (Stal et al., 2003; Jodłowska and Śliwińska, 2014) stating that this is caused by phycobilisomes, which are structural components of picocyanobacteria PSII photosystem. The presence of PCY cells throughout the whole euphotic water column was also reported in limnological studies (Becker et al., 2004, Callieri, 2007).

The discrepancies between the strains ecophysiology derived in this study amplified the need for in-depth investigation of three strains separately. What is more, according to the author's best knowledge, Baltic brown strain (BA-132) is the least recognized strain out of three analyzed *Synechococcus* sp. strains, so far. Stal et al. (2003) and Haverkamp et al. (2008)

pointed to its inhabitation in the Baltic Sea but did not give its characteristics in detail. In the recent research more detailed investigation on BA-132 was provided (Jodłowska and Śliwińska, 2014). Nonetheless, the autecology issue of this strain still requires careful studies. The present paper derives the new knowledge on the BA-132 responses to changing ecological conditions. What is more, the study places BA-132 among the other *Synechococcus* sp. strains and compares their ecophysiology pointing to significant differences between these organisms.

The study of Baltic picoplankton ecophysiology is also of a great importance in the context of climate change. According to Belkin (2009), the Baltic Sea is among the Large Marine Ecosystems (LME), where the most rapid warming is being observed (the increase in SST between 1982 and 2006 > 0.9°C). Moreover, there are studies pointing to an increase of average winter temperatures in northern Europe by several degrees by the year 2100 (Meier, 2002). These along with the presented results, which suggest that all analyzed strains of *Synechococcus* sp. were positively affected by T can be a strong argument for further numerical research on examining the effect of long-term positive temperature trend on the abundance of PCY in the Baltic Sea (the need for picoplankton model representation). What is more, the feedback relation, which is the surface most layer being warmed up by irradiance trapped in the cells of phytoplankton may derive interesting conclusions on the functioning of the ecosystem and the living organisms being the internal source of heat in the marine medium.

The observation that T increase had a positive impact on all strains' number of cells is also consistent with field studies, which indicate the seasonal cycle of PCY maximal abundances (Flombaum et al., 2013; Dutkiewicz et al., 2015; Worden and Wilken, 2016). Hajdu et al. (2007) showed that during the decline phase of Baltic cyanobacterial blooms in late summer, unicellular and colony-forming picocyanobacteria increased in abundance. Mazur-Marzec et al. (2013) indicated that the contribution of PCY biomass in total summer cyanobacterial biomass was usually high and ranged from 20% at the beginning of July to 97% in late July and August. Moreover, Paczkowska et al. (2017) pointed to the abundance of 40-90% in the summertime in the Baltic Sea and to PCY being a dominant size group in all Baltic basins. Stal et al. (1999) reported that 65% of the phytoplankton-associated Chl *a* concentration in the Baltic Proper during late summer belonged to picoplankton, while the second most dominant group was nitrogen-fixing cyanobacteria (*Aphanizomenon* sp., *Dolichospermum* sp. and *Nodularia* sp.). Contrary to that, there were also some reports regarding high PCY abundance in the wintertime. For instance, during the winter–spring period, PCY was the second most dominant fraction in the Baltic Sea (Paczkowska et al., 2017). The present study showed that PCY can survive and grow also in low T and PAR conditions, which is consistent to the finding of Paczkowska et al. (2017).

The studies of autecology of the PCY community and an understanding of its response to main environmental factors is an important step in recognizing the phenomenon of PCY blooms in marine environments. Additionally, the laboratory experiments became a foundation in developing a new approach to Baltic Sea phytoplankton modeling - development of pico-bioalgorithm describing PCY growth, which may enable long-term numerical studies on the response of PCY to changing environment.

5 Conclusions

Discrepancies in number of cells, pigmentation changes, Chl *a* fluorescence and photosynthesis characteristics implied that BA-120, BA-124 and BA-132 should be studied and examined separately.

Nonetheless, there were also fixed features referring to all analyzed strains, reasoning the association these features with *Synechococcus* as a species, in general. For instance, according to the derived results, PAR and T played a key role in the life cycle of all three strains. Additionally, the positive impact of salinity on the number of cells was observed in each culture. Another similarity was the prevalence of one of photoacclimation mechanisms, which was the change in size of PSU. This second most frequent type was altering of accessory pigments and the least frequent was the change in PSU number.

Contrary to that, the main differences were: different responses of number of cells to respective environmental conditions in different cultures; various photoacclimation mechanisms observed; and different changes in pigmentation.

According to the latest research, PCY are a great contributor to total primary production in the Baltic Sea and may contribute to summer cyanobacteria bloom at a high degree. This explains the authors' motivation to lead an in-depth investigation on Baltic PCY response to a changing environment. The present research is a first step on the way to deriving new knowledge on *Synechococcus* sp. ecophysiology and is a foundation for further studies.

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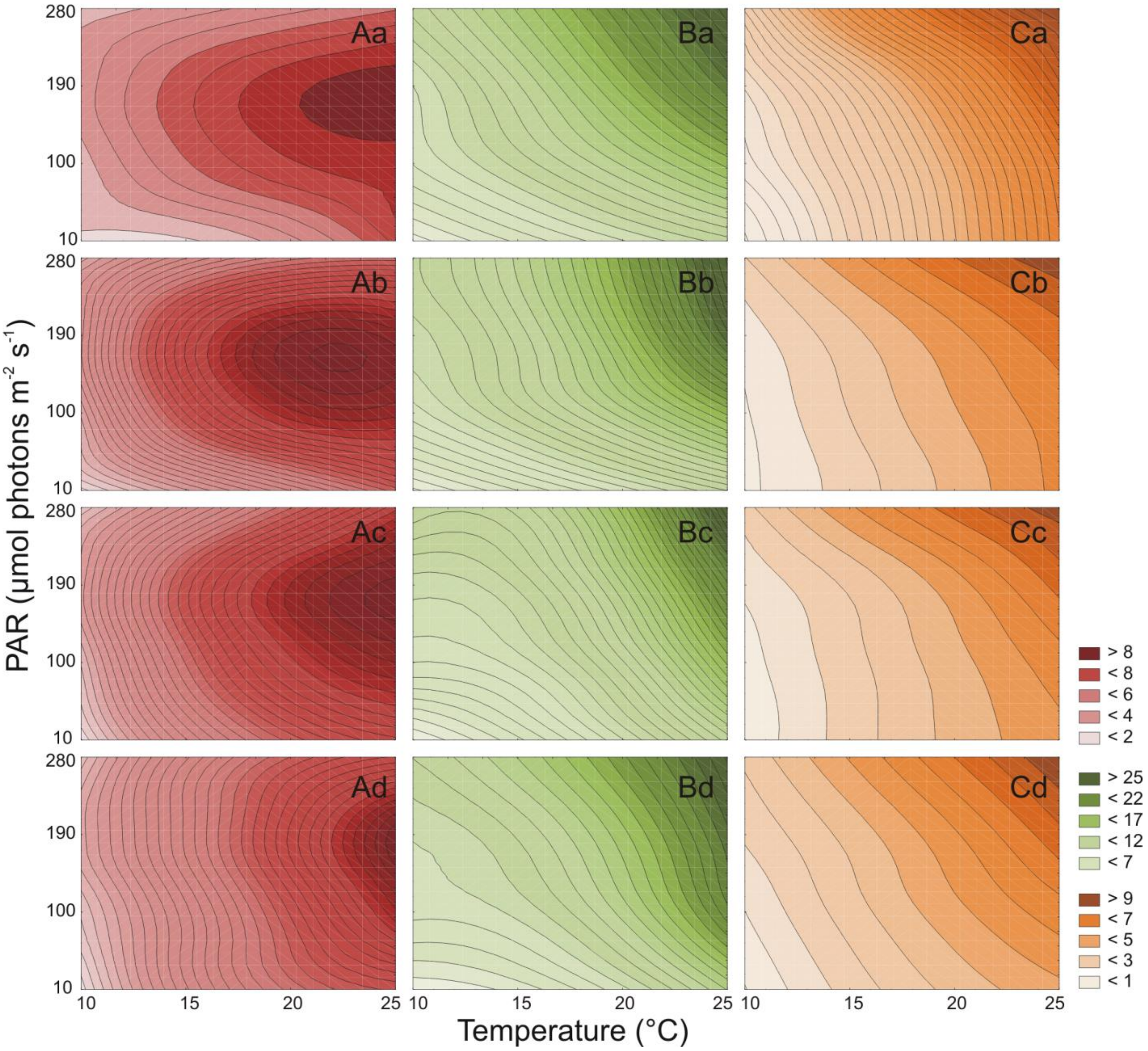

Figure 1. Cell number (10^6 cell mL^{-1}) for three *Synechococcus* sp. strains: BA-120 (A), BA-124 (B) and BA-132 (C) under different PAR and temperature conditions in 4 salinity mediums: 3 PSU (a), 8 PSU (b), 13 PSU (c) and 18 PSU (d).

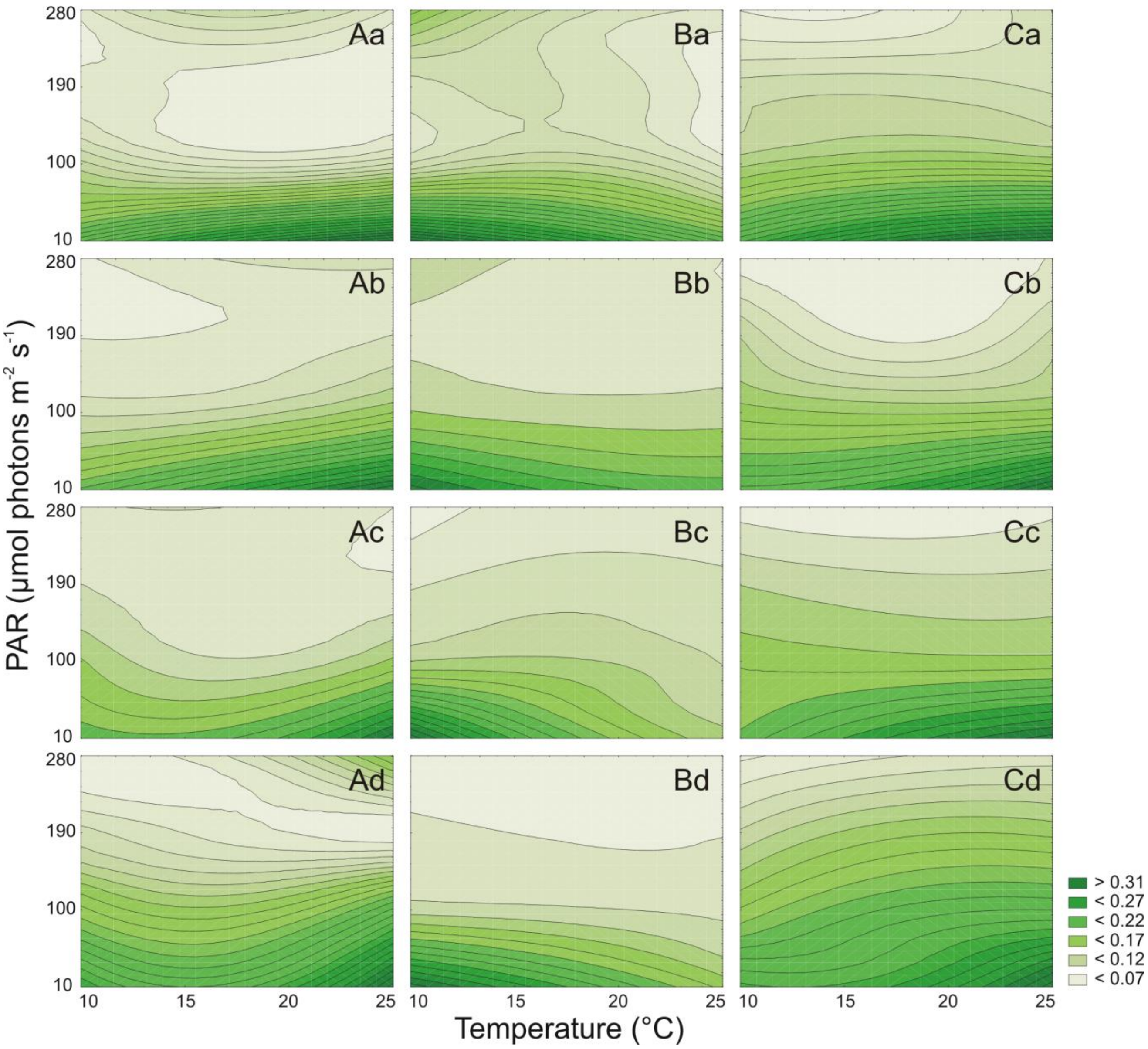

Figure 2. Cell-specific Chl *a* (pg cell^{-1}) changes for three *Synechococcus* sp. strains: BA-120 (A), BA-124 (B) and BA-132 (C) under different PAR and temperature conditions in 4 salinity mediums : 3 PSU (a), 8 PSU (b), 13 PSU (c) and 18 PSU (d).

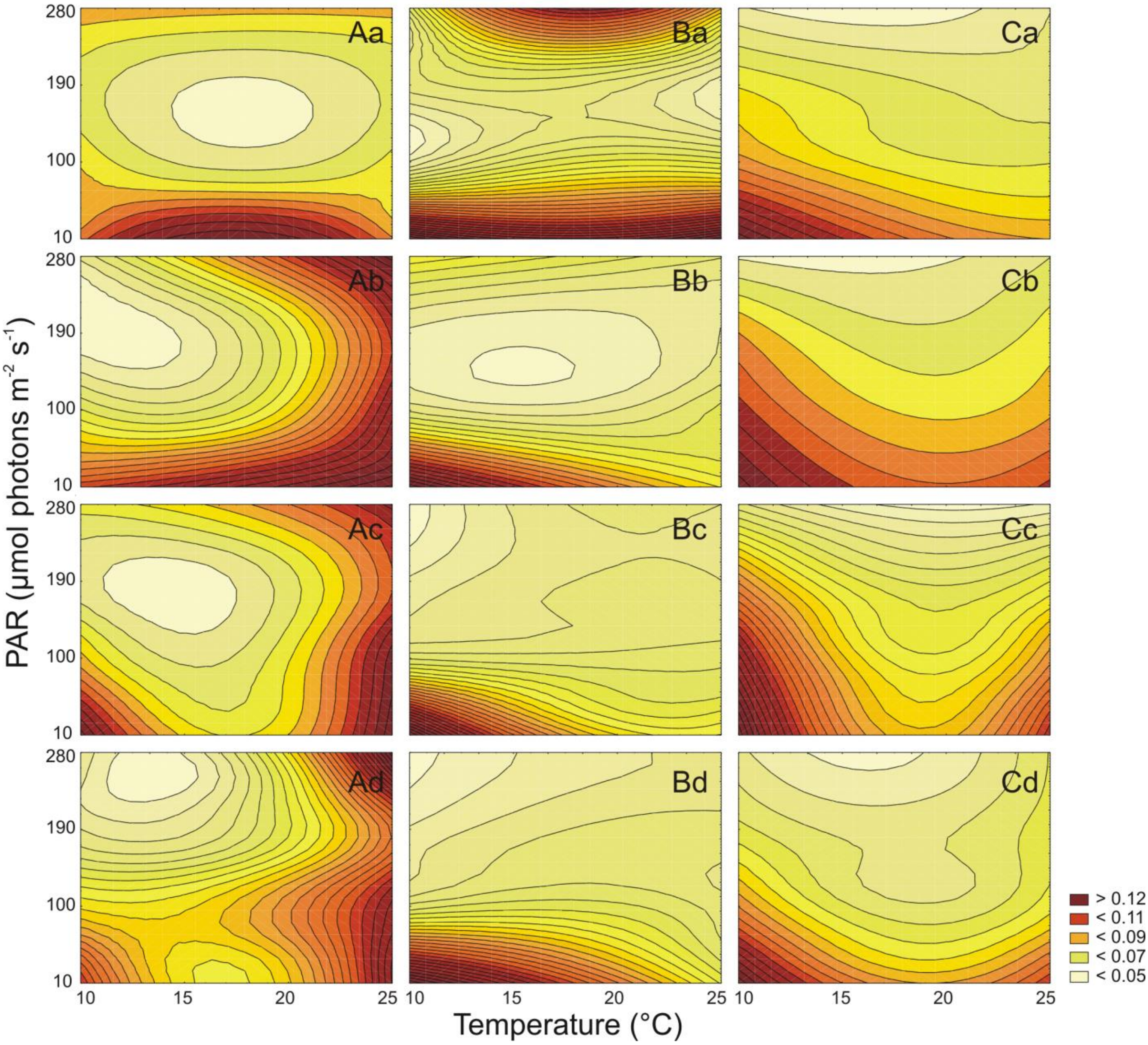

Figure 3. Cell-specific Car (pg cell^{-1}) changes for three *Synechococcus* sp. strains: BA-120 (A), BA-124 (B) and BA-132 (C) under different PAR and temperature conditions in 4 salinity mediums: 3 PSU (a), 8 PSU (b), 13 PSU (c) and 18 PSU (d).

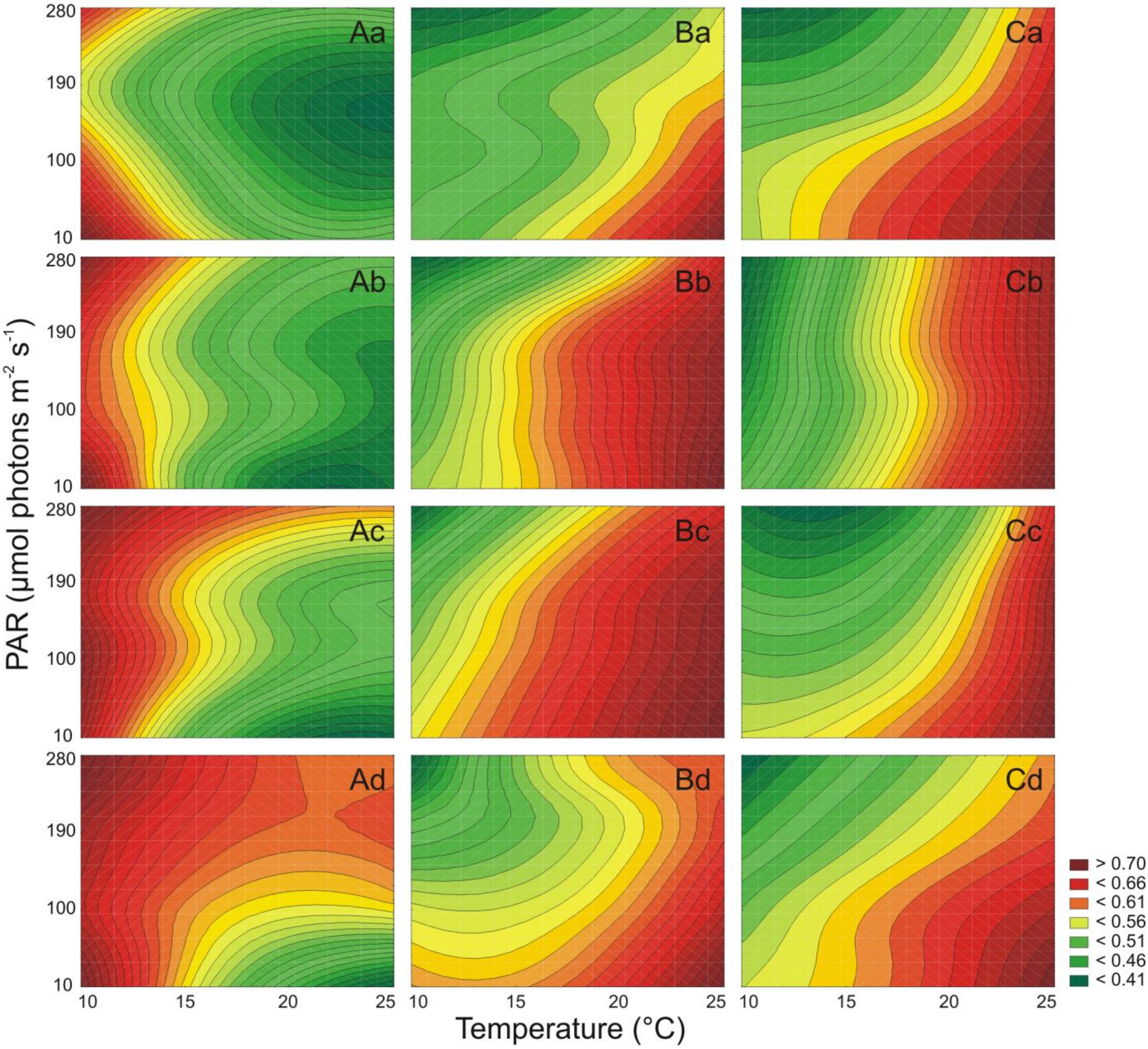

Figure 4. The maximum photochemical efficiency of PSII in the dark-adapted state (F_v/F_m) for three *Synechococcus* sp. strains: BA-120 (A), BA-124 (B) and BA-132 (C) under different PAR and temperature conditions in 4 salinity mediums: 3 PSU (a), 8 PSU (b), 13 PSU (c) and 18 PSU (d).

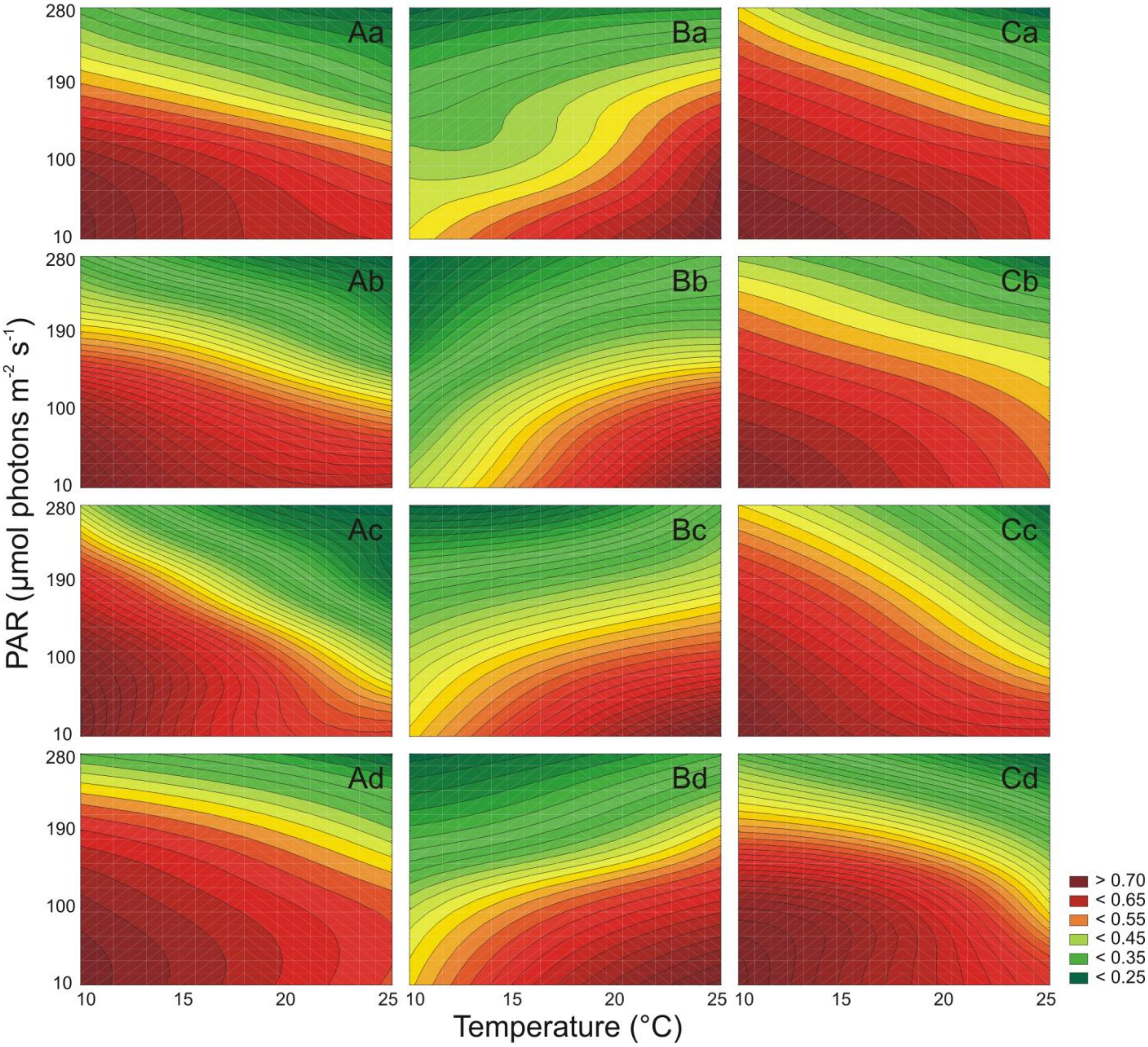

Figure 5. The photochemical efficiency of PSII under actinic light intensity (ΦPSII) for three *Synechococcus* sp. strains: BA-120 (A), BA-124 (B) and BA-132 (C) under different PAR and temperature conditions in 4 salinity mediums: 3 PSU (a), 8 PSU (b), 13 PSU (c) and 18 PSU (d).

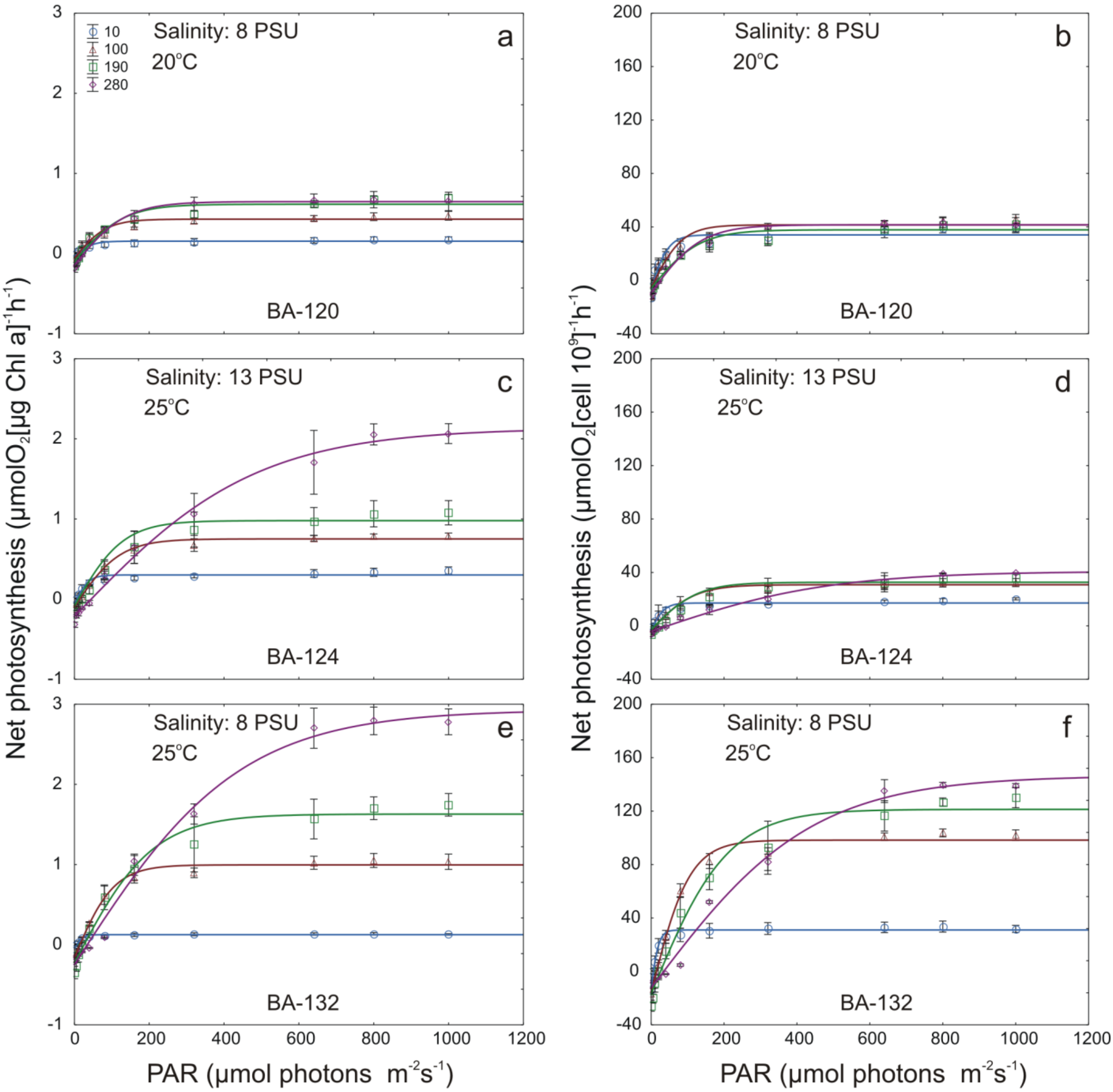

Figure 6. Selected Chl *a* - specific and cell-specific (right side and left side panel, respectively) net photosynthetic–light response curves for three *Synechococcus* sp. strains: BA-120 (a, b), BA-124 (c, d) and BA-132 (e, f) strains. Curves present examples of three types of photoacclimation observed for *Synechococcus* sp. and these are as follows: change in number of photosynthesis units (PSU) (a, b), change in size of PSU (c, d) and change in accessory pigments activity (e, f).

Table 1. Photoacclimation types (mechanisms) for three *Synechococcus* sp. strains: BA-120, BA-124 and BA-132 at different ecological conditions. OTHER stands for altering of accessory pigments activity or changes in enzymatic reactions; PSUsize stands for the change in PSU sizes; PSUno. stands for the change in PSU number. The symbols of labels indicate the strain for which the mechanism is observed and are as follows: [red] for BA-120, [green] for BA-124 and [brown] for BA-132.

CONDITIONS	Salinity 3 PSU	Salinity 8 PSU	Salinity 13 PSU	Salinity 18 PSU
10°C	PSUsize [brown]	OTHER [red] PSUsize [green] PSUsize [brown]	PSUsize [red] OTHER [red] OTHER [green]	OTHER [red] PSUsize [green] PSUsize [brown]
15°C	-	PSUsize [green]	OTHER [red] PSUsize [green] OTHER [brown]	PSUsize [brown]
20°C	-	PSUno. [red] OTHER [green] PSUsize	PSUsize (or OTHER) [red] OTHER [green] PSUsize	PSUsize [green]
25°C	OTHER [red] PSUsize [brown]	PSUsize [red] PSUsize [green] OTHER [brown]	PSUsize [red] PSUsize [green] PSUsize [brown]	PSUsize [green] PSUsize [brown]