Assessing Potential for Chromatic Acclimation in Oxygen Deficient Zone *Synechococcus*

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Abstract: *Synechococcus* are a genus of ubiquitous marine cyanobacteria that play an important role in global carbon cycling. *Synechococcus* are abundant in oxygen deficient zones (ODZs)—expanding areas of the ocean where oxygen concentrations drop below 10 nM O_2—where they fix carbon and introduce trace amounts of oxygen through photosynthesis to fuel aerobic respiration. *Synechococcus* can be grouped into different pigment types based on the makeup of the phycobilisome, a photosynthetic light-harvesting complex. Marine *Synechococcus* are predominantly either blue-light specialists, green-light specialists, or light-generalists. Light generalists undergo a process called chromatic acclimation where their phycobilisome structure is modified in response to changing light conditions allowing maximal growth under different colors of light which provides an advantage as a photosynthetic cell is moved throughout the upper water column. In this study, I use 10 strains of Clade 1 and CRD1 *Synechococcus* isolates and metagenomic data to determine the abundance, diversity, and potential for chromatic acclimation of *Synechococcus* in the Eastern Tropical North Pacific (ETNP) ODZ. I performed growth experiments on the Synechococcus isolates under white, blue, and green light finding that seven of the strains were able to chromatically acclimate while three were blue-light specialists. Through phylogenetic analysis, I found that *Synechococcus* in the ETNP ODZ fall into eight distinct groups that constitute 2 – 17% of the microbial community in the upper 50 meters of the water column. These results indicate that *Synechococcus* capable of chromatic acclimation are present and possibly abundant in the ETNP ODZ, comprising a potentially important contribution to cryptic oxygen cycling supporting aerobic heterotrophic communities.

Plain Language Summary:

Synechococcus are a widespread and abundant group of photosynthetic bacteria that account for approximately 17% of marine carbon fixation and oxygen production. They are abundant in

oxygen deficient zones (ODZs)—areas of the global ocean where oxygen concentrations in the water become undetectable and practically zero. As ocean temperatures rise due to human-driven climate change, ODZs are expected to expand, reducing habitat for pelagic fishes, and increasing ocean-acidification related stress. *Synechococcus* abundances are also expected to expand, potentially adding more oxygen to ODZs. In this study, I use 10 distinct types of *Synechococcus* isolated from the Eastern Tropical North Pacific ODZ to assess their potential for chromatic acclimation, or the ability to change their ratio of a blue-light and green-light absorbing pigment. I found that seven of the *Synechococcus* isolates can undergo this process, while the other three have a high, but unchanging amount of the blue-light absorbing pigment. This indicates that these *Synechococcus* may be adapted to living in the ODZ and may have unique ways to survive the low-oxygen, expanding environment.

Introduction: Phytoplankton are ubiquitous in surface waters of the ocean and play a crucial role in global carbon cycling (Rii et al., 2016). Photosynthesis is performed by phytoplankton in the ocean which results in the fixation of carbon—the biological transformation of inorganic carbon into organic carbon molecules. Fixed carbon is incorporated into phytoplankton biomass and can be consumed by heterotrophs effectively fueling much of the life on Earth. Roughly half of net primary production, the difference between an autotroph's energy fixation and its respiration, that occurs on Earth is due to phytoplankton (Field et al., 1998). The two cyanobacteria genera *Prochlorococcus* and *Synechococcus* are the most abundant phytoplankton, accounting for approximately 25% of oceanic net primary production (Flombaum et al., 2013; Huang et al., 2012; Liu et al., 1997). In mid-latitude regions of the ocean, *Synechococcus* is the

dominant phytoplankton contributing an estimated 17% of oceanic net primary production alone (Flombaum et al., 2013; Liu et al., 1997).

Members of the genus *Synechococcus* are divided into distinct clusters, or clades, based on conserved but slightly variable genetic regions such as the 16S ribosomal RNA gene (Dufresne et al., 2008), the 16S-23S internally transcribed spacer (ITS) (Rocap et al., 2002), and a series of other genes present in all known *Synechococcus*. Individual clades have different physiologies and global distributions and affect biogeochemical cycles differently (Ahlgren & Rocap, 2012; Wang et al., 2022). While clades are distinct, there is still great diversity between individual strains within a clade. For example, strains within a single clade may have genes encoding for different light-absorbing pigments and thus grow differently under the same light conditions by absorbing and utilizing different qualities (wavelengths) of light.

Synechococcus use a combination of blue and red-light absorbing monovinyl chlorophyll *a*; blue, green and ultraviolet absorbing zeaxanthin and β-carotene; and the variable phycobilisome which consists of phycobiliproteins rods that attach to light-absorbing phycobilins. The light absorbing properties of the phycobilisome are determined by the *Synechococcus*'s pigment type. Pigment type 1 (PT1) rods are composed solely of phycocyanin bearing the red-light absorbing phycocyanobilin (PCB) (Six et al., 2007). Pigment type 2 (PT2) is composed of a fixed ratio of phycocyanin and phycoerythrin-I attached to PCB and the green-light absorbing phycoerythrobilin (PEB) (Six et al., 2007). Finally, pigment type 3 (PT3) phycobilisomes are composed of phycocyanin, phycoerythrin-I, and phycoerythrin-II rods that can attach to PCB, PEB, or blue-light absorbing phycocourobilin (PUB).

Synechococcus that exhibit subtypes PT3a-c have a fixed ratio of PUB to PEB ranging from low (~0.4 PUB:PEB; PT3a), intermediate (~0.8 PUB:PEB; PT3b), and high (greater than

1.7 PUB:PEB; PT3c) (Six et al., 2007). Subtype PT3d *Synechococcus* can change the ratio of the PUB and PEB within their phycobilisomes in response to changing light quality to grow maximally under different combinations of blue and green light in a process known as type IV chromatic acclimation (Palenik, 2001). Cyanobacteria that can chromatically acclimate, including some strains of *Synechococcus*, are considered light generalists that photosynthesize more efficiently relative to non-chromatically acclimating, specialist *Synechococcus* at high light intensities (Lovindeer et al., 2021). At light intensities less than ~120 µmol photons m^{-2} s^{-1} under a single quality of light, specialist *Synechococcus* have higher light efficiencies than generalists (Lovindeer et al., 2021). For example, a blue-light specialist will have a higher growth rate than a light-generalist under lower blue-light intensities.

The genetic potential for chromatic acclimation in marine *Synechococcus* is controlled by one of two genomic islands—areas of the genome obtained through horizontal gene transfer—CA4-A and CA4-B (Humily et al., 2013). Specifically, these genomic islands are hypothesized to be inserted by tycheposon-like mobile DNA elements (Grébert et al., 2022) that contain a gene that attaches PEB to phycoerythrin-II and converts it to PUB (Humily et al., 2013). Since these regions can be horizontally transferred, the ability to chromatically acclimate cannot be determined by taxonomic assignment.

Increases in sea surface temperature due to anthropogenic climate change are predicted to cause a 14% increase in *Synechococcus* abundance by the end of the 21st century making it important to understand *Synechococcus* photophysiology (Flombaum et al., 2013). Rising ocean temperatures are also causing the expansion of oxygen deficient zones (ODZs) due to the inverse relationship between gas solubility and water temperature. ODZs are large, naturally-occurring regions in the world's ocean where oxygen concentrations drop below 10 nM O_2. Alternate

electron acceptors such as nitrate, sulfate, and ammonia are used to fuel anaerobic respiration in the absence of oxygen, making ODZs important to the biogeochemical cycling of nitrogen and sulfur despite their relatively small size (Bertagnolli & Stewart, 2018). ODZs are often on the west side of continents and are formed from a combination of sluggish water circulation and the respiration of sinking organic particles by heterotrophic microbes (Stramma et al., 2010; Wright et al., 2012). In some parts of ODZs, enough light penetrates through the water column that a secondary chlorophyll maximum can occur. *Prochlorococcus*, a sister clade of *Synechococcus*, dominate in the ODZ core and the secondary chlorophyll maximum. *Synechococcus*, however, are the most abundant cyanobacteria in the surface and primary chlorophyll maximum in coastal ODZs (Lavin et al., 2010). While *Synechococcus* are found at low abundances in the secondary chlorophyll maximum, individuals that can chromatically acclimate to more effectively absorb blue light may be more abundant than metagenomic results indicate. The combined growth of ODZs and predicted increase in *Synechococcus* abundances make ODZs an important region to study *Synechococcus*.

With both ODZs predicted to expand and rising sea-surface temperature leading to increased *Synechococcus* abundance, it is important to determine where in the ODZ water column *Synechococcus* are most successful. By better understanding how *Synechococcus* contribute to carbon and oxygen cycling in ODZs, we can better predict how ODZs contribute biogeochemical cycles as they continue to expand. I hypothesize that strains of *Synechococcus* isolated from the secondary chlorophyll maximum within the ETNP ODZ can chromatically acclimate to grow maximally using differing light qualities available deep in the water column.

Methods:

***Synechococcus* isolation and characterization:**

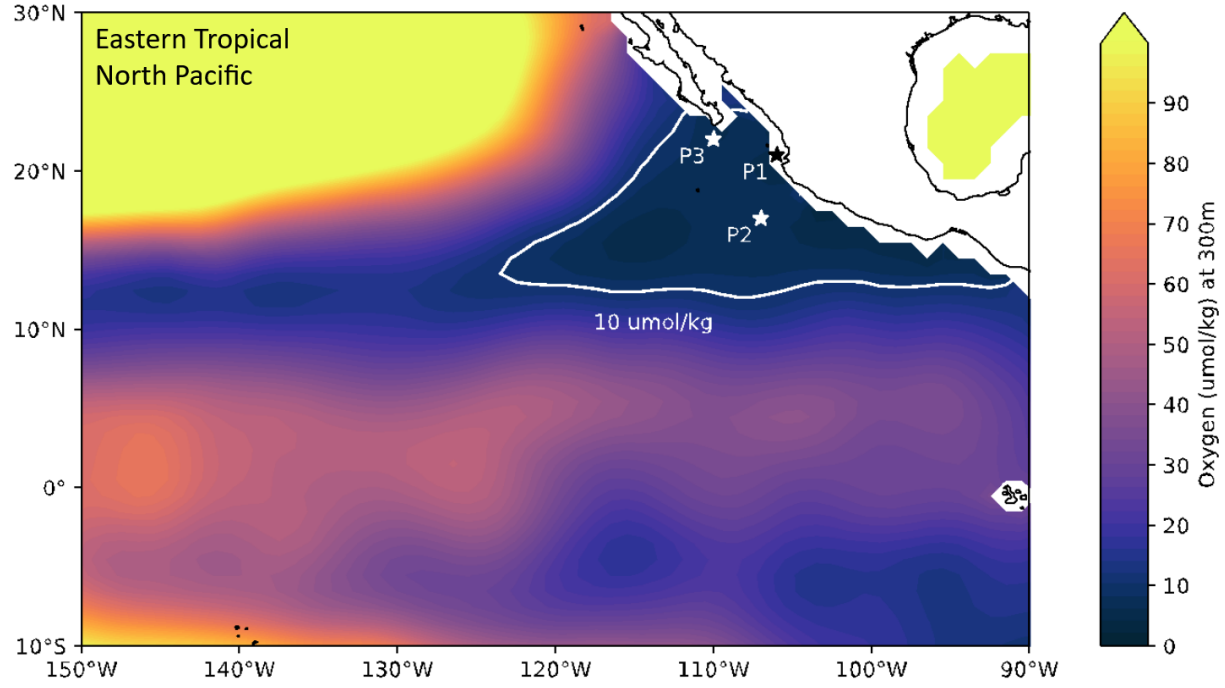

Figure 1 – The Eastern Tropical North Pacific ODZ with a heatmap of dissolved oxygen concentrations at 300 meters overlayed. Each of the three stations are indicated by a star and the station name.

Synechococcus strains were isolated from the offshore ETNP ODZ secondary chlorophyll maximum (P2; Figure 1) in April 2018 and October 2019 during the RR1804-5 and KM1919-20 cruises, respectively. Seawater samples from Niskin bottles were filtered through two 2 µm filters to remove larger organisms, aliquoted into 15 mL culture tubes containing AMP1 artificial seawater (Moore et al., 2007), and maintained under 15-20 µmol photons m^{-2} s^{-1} of white light. Flow cytometry was performed to determine the presence of *Synechococcus* by their emitted fluorescence and scatter. Following a modified phenol-chloroform DNA extraction (Chan et al., 2001), the 16S-23S rRNA internally transcribed spacer (ITS) regions were PCR amplified and Sanger sequenced by Azenta Life Sciences Genomics in Seattle.

Clade identity was determined via phylogenetic analysis of the DNA sequence of each strain's ITS. Sequences were then aligned using MAFFT version v7.055b (Katoh & Standley, 2013) and placed on a phylogenetic tree using IQ-Tree version 2.2.0.3 (Hoang et al., 2018;

Kalyaanamoorthy et al., 2017; Minh et al., 2020). Visualization was performed with iTOL version 6.8.1 (Letunic & Bork, 2021).

Growth Experiments:

Growth experiments were performed on 10 strains of *Synechococcus* chosen based on their clade identities. Each strain was grown under 30 μmol photons m^{-2} s^{-1} of white, blue, and green light at 20ºC. The quality of light was controlled by placing the strains within boxes made from blue and green film (#721 Berry Blue, #139 Primary Green; norcostco.com/lee-filters). Growth rates were determined by reading each strain's fluorescence of chlorophyll *a* as a proxy for cell abundance using a 10-AU Fluorometer (Turner Designs). Each strain was transferred when its fluorescence read approximately 20% of its stationary value. After at least three transfers with consistent growth as determined by visual inspection of each strain's growth curves, average growth rates were calculated. ANOVA was then performed to ensure that differences in each strain's specific growth rate were not statistically significant. ANOVA and Tukey-Kramer tests were also performed to determine whether there were statistical differences between each strain's average growth rate.

Absorbance and Excitation Spectra:

Each strain's absorbance spectra under white, blue, and green light was determined from a concentrated subsample read on a Synergy H1 Microplate Reader (BioTek Instruments) from 400 – 700 nm with a step size of 1 nm. Absorbance spectra were normalized to the maximal absorbance of chlorophyll *a* (Chl a_{max} = 439 nm). Excitation spectra for each light condition were also generated from subsamples of each strain and read on the microplate reader with an excitation range of 400 – 600 nm, an emission wavelength of 585 nm, and a step size of 1 nm. Each excitation spectra was normalized to its maximum value. From each excitation spectra, the

ratio of the maximal fluorescence of PUB (PUB_{max} = 495 nm) to PEB (PEB_{max} = 545 nm) was used to determine pigment type.

Environmental ODZ Data:

Environmental DNA reads were sampled from the ETNP ODZ as a part of the April 2018 RR1804-5 POMZ cruises by the Rocap Lab. PacBio long reads containing the 16S ribosomal RNA gene were taxonomically identified using the SILVA ribosomal RNA database (Quast et al., 2013). Sequences identified as belonging to chloroplasts were removed from further analysis. Sequences identified as belonging to the phylum Cyanobacteria were aligned using ssu-align version 0.1.1 (Nawrocki, 2009) with the --global flag. Chimeric sequences were removed using the *alakazam* R package (Gupta et al., 2015). Sequences were then placed on a phylogenetic tree with a GTR+FO model using RAxML-NG (Kozlov et al., 2019) with reference sequences belonging to each clade of *Synechococcus* to determine identity and abundance of each clade. Abundance was then normalized to the total number of 16S rRNA reads present at each sampled depth.

CTD data were also collected as a part of the cruise. Temperature was measured using a SBE-9 CTD (Sea-Bird Scientific). Oxygen was measured using a SBE-43 dissolved oxygen sensor (Sea-Bird Scientific). Fluorescence was measured using a SCF3781 chlorophyll fluorometer (Seapoint). Photosynthetically active radiation (PAR) was measured using a LI-190R quantum sensor (Li-Cor).

Results:

Synechococcus Clade Identity:

Figure 2 – An ITS phylogenetic tree generated from reference Synechococcus sequences, metagenome assembled genomes (MAGs), and ODZ isolates. Black arrows indicate strains chosen for further analysis. Blue circles indicate bootstrap values above 80%. Blue highlighted sequences taken from ETNP ODZ MAGS (Fuchsman et al., 2017). Yellow highlighted sequences are all isolates taken from the ETNP ODZ in 2018 and 2019.

Synechococcus isolates from the ETNP ODZ were restricted to members of clades CRD1 and Clade 1 (Figure 2). From these, four strains belonging to CRD1 and six strains from Clade 1

were chosen. Isolates in Clade 1 grouped into three subgroups, two strains from each of the subgroups were used (Figure 2).

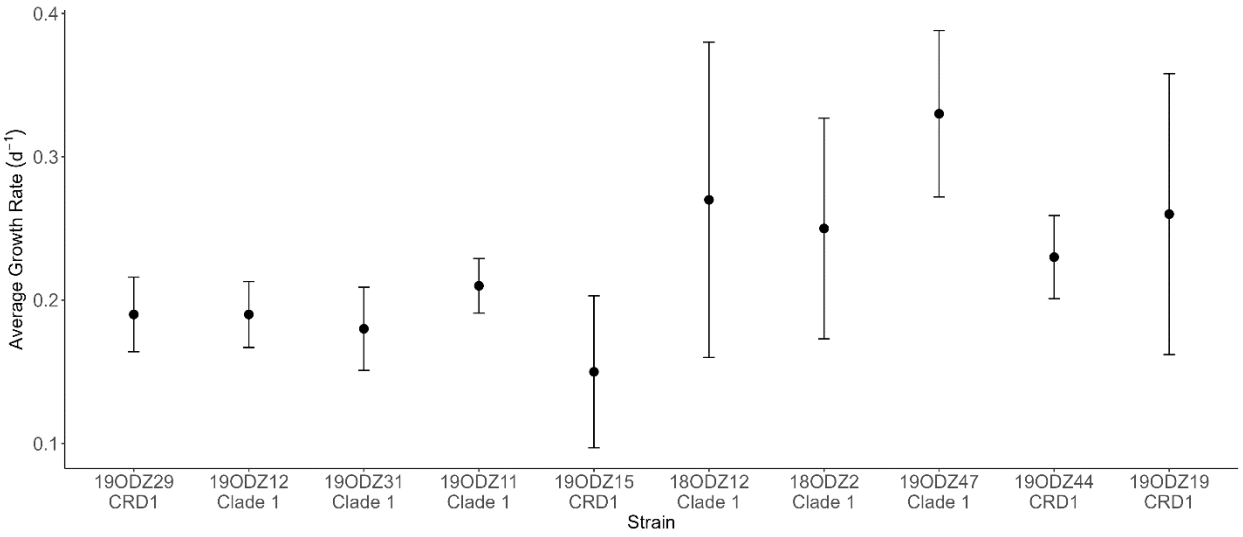

Figure 3 – Average growth rates of each Synechococcus strains under 30 µmol photons m^{-2} s^{-1} of white light. Error bars represent the standard deviation between consecutive transfers. There were not statistically significant differences in growth rates between strains (Tukey HSD; $p >> 0.05$).

Growth Experiments and Pigment Analysis:

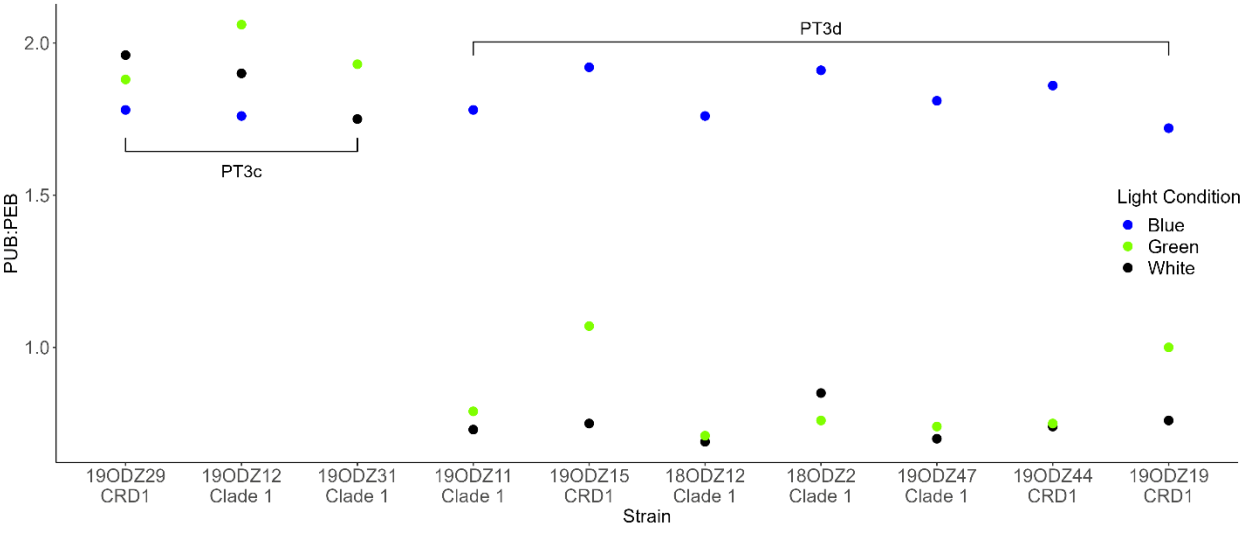

Figure 4 – Changes in PUB:PEB under blue, green, and white light conditions. PT3c strains are considered blue-light specialists with a fixed PUB:PEB ratio regardless of light condition. PT3d strains perform type-IV chromatic acclimation by changing their PUB:PEB under different light conditions.

Synechococcus growth rates under white light were variable, with averages ranging from 0.15 to 0.33 d^{-1} (Figure 3; Table 1), however, there were not statistically significant differences in growth rates between strains (Tukey HSD; $p >> 0.05$) . Growth rates under blue and green light were not calculated. PUB:PEB from excitation spectra of blue, green, and white acclimated cultures indicate that three of the 10 were subtype PT3c, with PUB:PEB greater than 1.7 under all three light conditions (Figure 4; Table 1). The other seven cultures belong to subtype PT3d with variable PUB:PEB under each light condition (Figure 4; Table 1).

Table 1 – Characteristics of each *Synechococcus* strain. Clade identity determined by phylogenetic analysis of the ITS sequence. PUB:PEB ratios determined from whole cell fluorescence excitation spectra. Growth rates determined from fluorescence growth experiments calculated via ANOVA. Number of transfers indicate the number of growth rates used to calculate the average growth rates of each strain.

Strain	Clade	White Light PUB:PEB	Blue Light PUB:PEB	Green Light PUB:PEB	Pigment Type	Growth Rates under white light (d^{-1}) ± SD	Number of Transfers
19ODZ29	CRD1	1.96	1.78	1.88	PT3c	0.19 ± 0.026	3
19ODZ12	I	1.90	1.76	2.06	PT3c	0.19 ± 0.023	3
19ODZ31	I	1.75		1.93	PT3c	0.18 ± 0.029	4
19ODZ11	I	0.73	1.78	0.79	PT3d	0.21 ± 0.019	6
19ODZ15	CRD1	0.75	1.92	1.07	PT3d	0.15 ± 0.053	3
18ODZ12	I	0.69	1.76	0.71	PT3d	0.27 ± 0.11	6
18ODZ2	I	0.85	1.91	0.76	PT3d	0.25 ± 0.077	4
19ODZ47	I	0.70	1.81	0.74	PT3d	0.33 ± 0.058	4
19ODZ44	CRD1	0.74	1.86	0.75	PT3d	0.23 ± 0.029	5
19ODZ19	CRD1	0.76	1.72	1.00	PT3d	0.26 ± 0.098	3

There were changes in the absorption spectra for each of the chromatically acclimating *Synechococcus* strain under each of the light conditions (Figure 5). There was a change in the relative height of the PUB and PEB peaks corresponding to a change in the expression of each of these pigments under white, blue, and green light (Figure 5). There were not differences in the absorption spectra of the blue-light specialists under the different conditions (Figure 5).

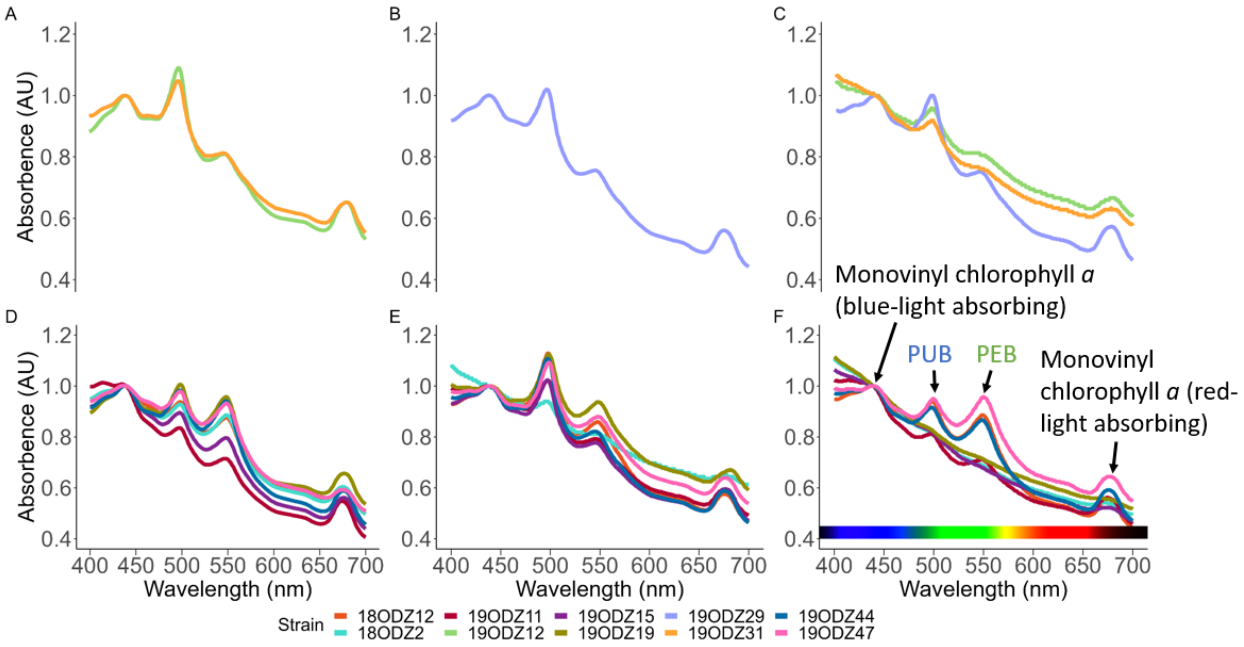

Figure 5 – Whole cell absorbance spectra for 10 strains of Synechococcus grown under approximately 30 µmol photons m^{-2} s^{-1} of white light (A, D), blue light (B, E), and green light (C, F). The top row (A-C) are the absorbance spectra of the three PT3c strains while the bottom row (D-F) are the spectra of the seven PT3d strains. The blue and red light absorbing peaks of monovinyl chlorophyll a are labeled as well as the blue-light absorbing phycourobilin (PUB), and green-light absorbing phycoerythrobilin (PEB). The legend shows the strain corresponding to each peak. Each absorbance spectra has been normalized to the maximal blue-light absorbance of chlorophyll *a*.

Environmental ODZ 16S rRNA Data:

Synechococcus in the ETNP ODZ were more abundant at the coastal station than the offshore station (Figure 6C). Within the coastal station, *Synechococcus* belonging to CRD1 were the most abundant group of Cyanobacteria present, accounting for approximately 10% of the microbial community (Figure 6C). *Synechococcus* were more abundant in the upper, oxygenated waters at the coastal station than *Prochlorococcus* (Figure 6A-C). At the offshore station, *Prochlorococcus* dominated at all depths, with *Synechococcus* only accounting for approximately 1% of the microbial community within the upper, oxygenated water (Figure 6D-F).

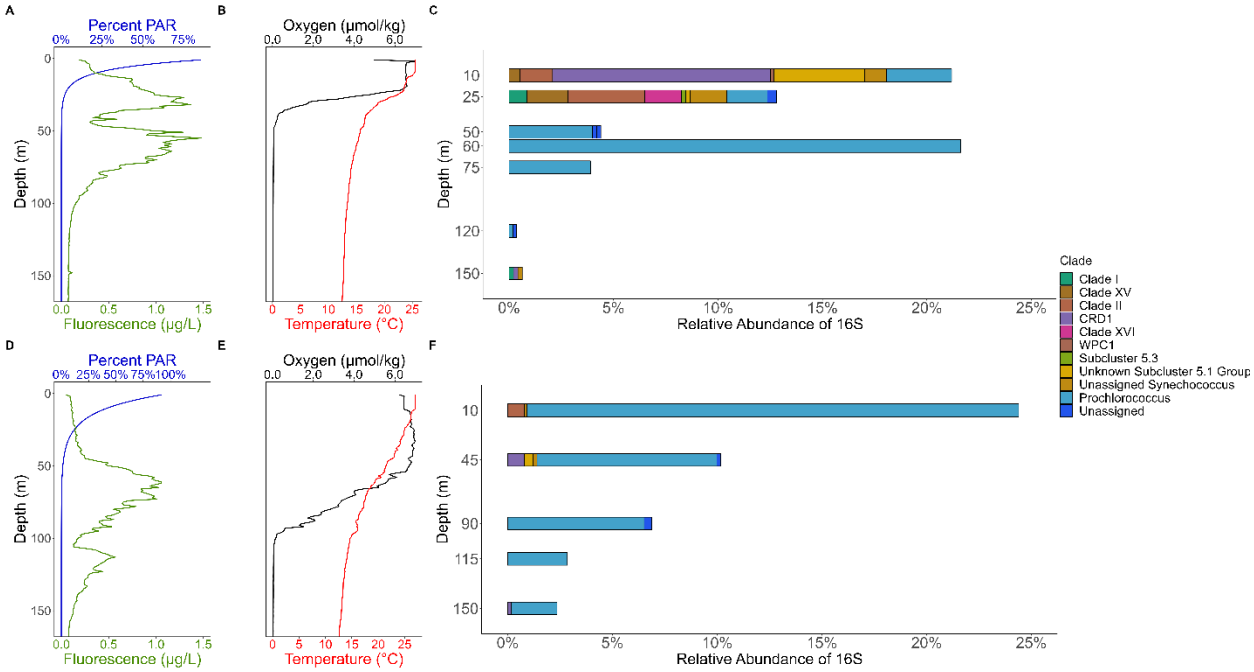

Figure 6 – **A.** Depth profile of percent photosynthetically active radiation (PAR) and fluorescence in the upper 150 m of the ETNP ODZ. **B.** Depth profile of oxygen and temperature at the same station. **C.** Depth profile focusing on the abundance—or the number of 16S rRNA gene reads in the DNA sample—and diversity of *Synechococcus* at a coastal station of the ETNP ODZ down to 150 m from 16S rRNA genes taken from unpublished Rocap Lab metagenomic data. Plots **A-C** are from a coastal station while **D-F** are from an offshore station.

Discussion:

I found that chromatic acclimating *Synechococcus* belonging to both Clade 1 and CRD1 are present in the ETNP ODZ secondary chlorophyll maximum (Figure 4; Table 1). This is consistent with metagenomic samples taken as a part of TARA Oceans (Sunagawa et al., 2020) which show a trend toward an increase in the relative abundance of chromatic acclimating *Synechococcus* in the deep chlorophyll maximum relative to the surface (Grébert et al., 2018). Chromatic acclimating *Synechococcus* were the dominant pigment type in deep chlorophyll maximum samples taken from the Eastern Tropical South Pacific ODZ by TARA Oceans (Grébert et al., 2018). Blue-light specialist strains are also present in the ETNP ODZ secondary chlorophyll maximum belonging to clades CRD1 and Clade 1 with PUB:PEB ratios comparable to other PT3c isolates such as WH8102 (Six et al., 2004; Toledo et al., 1999).

Synechococcus growth rates under white light in this study were inconclusive. There were not significant differences between any of the strain's growth rates (Figure 3). Qualitatively, it seems that the three blue-light specialists had less variable, but lower growth rates than the chromatically acclimating strains; this would be consistent with PT3d *Synechococcus* having a lower light-use efficiently relative to light-specialist strains (Lovindeer et al., 2021). While growth rates under blue and green light were not calculated in this study, it would be expected that the chromatic acclimating strains would have a higher growth rate relative to the blue-light specialists under green light, but a lower growth rate under blue light, again due to the lower light-use efficiency.

Secondary chlorophyll maximums usually occur where light is one percent of surface irradiance (Figure 6A, Figure 6D). In coastal ODZs, where the two chlorophyll maxima are shallower, PT3d *Synechococcus* may have a growth advantage over PT3c as mixing exposes cells to different qualities of light. In open-ocean areas of ODZs where the chlorophyll maxima are deeper, however, PT3c *Synechococcus* may have a growth advantage as blue-light becomes the dominant wavelength available for photosynthesis. While PT3d *Synechococcus* can exhibit high PUB:PEB, they also have a decreased light-use efficiency relative to blue or green-light specialists (Lovindeer et al., 2021). In well-mixed waters, however, the trade-off of a lower light use efficiency for chromatic acclimation may be beneficial.

Metagenomic data taken from the ETNP ODZ indicate that *Synechococcus* are only abundant in the in the upper, oxygenated, coastal waters of the ODZ (Figure 6A-C). This is consistent with environmental samples from the Eastern Tropical South Pacific which also indicate that *Synechococcus* have low abundances within the anoxic ODZ core (Lavin et al., 2010). However, the *Synechococcus* strains used in this study were isolated from the anoxic,

low-light secondary chlorophyll maximum of the offshore station. Clearly, there are *Synechococcus* present below the oxycline in ODZs. It is unknown, however, whether they are too low in abundance to be sampled through metagenomic approaches or if they are intermittently mixed to depth and not actively photosynthesizing. Given that each of the tested *Synechococcus* isolates were either blue-light specialists or light-generalists, *Synechococcus* may be a small, but active portion of the microbial community within the anoxic secondary chlorophyll maximum.

As demonstrated in this experiment and others (Grébert et al., 2018, 2022; Palenik, 2001), the ability to chromatically adapt is not restricted by taxonomic identity (Figure 4, Table 1). While the 16S rRNA gene is sufficient to taxonomically identify *Synechococcus* clades, we cannot determine pigment type by this method. Future work should explore the distribution of chromatically acclimating *Synechococcus* in ODZs by identification of the CA4 genomic islands. While not all *Synechococcus* that possess these islands have the ability to chromatically acclimate (Humily et al., 2013), this approach combined with the identification of other phycobilisome genes found in chromatic acclimating *Synechococcus* strains may provide a more complete view of the photophysiology of *Synechococcus* in ODZs.

Conclusion:

Synechococcus are an important group of picophytoplankton that account for approximately 17% of marine primary productivity. In ODZs, *Synechococcus* introduce trace amounts of oxygen in anoxic ODZ waters immediately used by heterotrophic organisms. Rising ocean temperatures due to anthropogenic climate change are expected to cause an increase in *Synechococcus* abundance and an expansion of ODZs. The isolated *Synechococcus* strains examined in this study belonged to PT3c and PT3d. Both groups have the potential for high

PUB:PEB allowing them to capture blue wavelengths of light that can penetrate deep into the water column. Combining these results with the environmental DNA results, PT3c and PT3d *Synechococcus* may be present in the anoxic ODZ core, but are not abundant enough to be detected by DNA sampling.

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