Upper Ocean Dynamics Select for Synechococcus Light Color Generalists

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Abstract

The ocean has many underwater light niches, but the selection pressure for chromatic acclimaters (generalists) compared to blue or green-specialists is not well understood. Here, we tested the hypothesis that changes in ocean spectra brought about by mixing on the order of days preferentially selects for generalists within a *Synechococcus* population. We investigated ocean conditions that led to high proportions of *Synechococcus* generalists versus specialists in a model ocean column, and compared simulations with *in situ* metagenomic and physical oceanographic data from major Bio-GO-SHIP cruises, supplemented with GEOTRACES and TARA Oceans, as well as the GOOS Argo Program and sea surface height from AVISO. We found that greater mixed layer depths selected for generalists in simulated *Synechococcus* populations, but explained only 14% of the partitioning between strategies in situ. Rather, variability due to upwelling and ocean fronts had larger effects, explaining ~40%of the partitioning between *Synechococcus* generalists and specialists in the ocean. Physical oceanographic drivers therefore offer a significant selection pressure on marine *Synechococcus* light-harvesting strategies. Our results motivate further study of the *in situ* light environments of upwelling zones and ocean fronts, which are currently understudied as potential light-driven niche habitats.

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10							
11	Key Points:						
12 13	• Deep mixing, upwelling zones, and surface ocean gradients are important niches for chromatic acclimating marine cyanobacteria.						
14 15	• A high proportion of blue/green acclimaters at ocean fronts motivates future work on the internal spectral variability of these regions.						

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- 19 (generalists) compared to blue or green-specialists is not well understood. Here, we tested the
- 20 hypothesis that changes in ocean spectra brought about by mixing on the order of days
- 21 preferentially selects for generalists within a Synechococcus population. We investigated ocean
- 22 conditions that led to high proportions of *Synechococcus* generalists versus specialists in a model
- 23 ocean column, and compared simulations with *in situ* metagenomic and physical oceanographic
- 24 data from major Bio-GO-SHIP cruises, supplemented with GEOTRACES and TARA Oceans, as
- 25 well as the GOOS Argo Program and sea surface height from AVISO. We found that greater
- 26 mixed layer depths selected for generalists in simulated *Synechococcus* populations, but
- explained only 14% of the partitioning between strategies in situ. Rather, variability due to
- 28 upwelling and ocean fronts had larger effects, explaining ~40% of the partitioning between
- 29 Synechococcus generalists and specialists in the ocean. Physical oceanographic drivers therefore
- 30 offer a significant selection pressure on marine *Synechococcus* light-harvesting strategies. Our
- 31 results motivate further study of the *in situ* light environments of upwelling zones and ocean
- 32 fronts, which are currently understudied as potential light-driven niche habitats.
- 33

34 Plain Language Summary

- 35 The variety of pigments used by cyanobacteria to capture light for photosynthesis increases the
- 36 colors of light available for use in the ocean. One genus of cyanobacteria, *Synechococcus*, can
- 37 change color to absorb either blue or green light (generalists), adding to the variety of light-
- 38 harvesting strategies. Though the reason for this color change is believed to be fluctuations in the
- 39 underwater blue/green light field, this has not been tested directly. Using a mathematical model
- 40 of the ocean column, we find the highest percentages of generalists in the *Synechococcus*
- 41 population in deep ocean mixed layers. Comparison of model results to actual distributions of
- 42 generalists indicate that deep mixing plays a smaller role than our model suggested, and that
- 43 upwelling zones, where water is vertically moved to the surface, and ocean fronts, where major
- 44 ocean currents meet, are also important habitats for higher percentages of *Synechococcus*
- 45 generalists in the ocean.
- 46

47 **1. Introduction**

48 The terms *generalist* and *specialist* in ecology refer to organisms with differences in

49 tolerance or preference for food or habitat—generalists having weaker preferences and wider

50 tolerances. Examples are abundant in the literature and range from generalist bird species able to

adapt to disturbed environments (Viol et al., 2012) to the broad feeding habits of fish in Arctic

- 52 lakes (Laske et al., 2018). Among photosynthetic organisms in aquatic environments, feeding
- 53 and habitat preferences translate into nutrient and light-color acquisition, or light intensity,

54 temperature, and salinity tolerances. In cyanobacteria, preferential use of specific wavelengths of 55 light in aquatic ecosystems provides a colorful example of generalists—strains able to change 56 pigmentation to maximally absorb one wavelength over another (chromatic acclimation). In 57 lakes, rivers, estuaries, and oceans, light attenuates exponentially with depth, and partitions into 58 colors depending on the composition of the water. Aquatic cyanobacteria must be adapted to use 59 these available colors. Examples include high turbidity and increased colored dissolved organic 60 matter (CDOM) in lakes that result in mostly red light for photosynthesis, or blue light 61 dominating in clear, deep, open ocean water (Holtrop et al., 2020; Stomp et al., 2007). When the 62 color of underwater light changes in an ecosystem, generalists can undergo acclimation (Stomp 63 et al., 2004) whereas specialists may undergo succession (Luimstra et al., 2020; Stomp et al., 64 2007).

65 To date, five types of chromatic acclimation strategies have been identified in coastal and in-land waters (Sanfilippo et al., 2019). All are performed by cyanobacteria containing 66 67 phycobiliprotein light-harvesting pigments, though at least one strategy involves removal of phycobilins in favor of chlorophyll-d (CA5). Strategies may include changes in the relative ratio 68 69 of phycobiliproteins (such as occurs in red and green light in CA2 and CA3), and rearrangement 70 of the phycobilisome core and attached chlorophylls (as in red & far/red light in CA6/FarLiP). 71 Blue/green chromatic acclimation (CA4, Palenik, 2001) is unique in that it is the only 72 acclimation type currently known to exist in the open ocean, is performed exclusively by 73 phycoerythrin-containing marine Synechococcus, and involves changes in the relative ratio of 74 chromophores attached to phycoerythrin, rather than a change in the ratio of the

75 phycobiliproteins themselves.

76 All Synechococcus CA4 generalists have phycobilisomes (light-harvesting structures that 77 house the phycobiliproteins) that contain phycocyanin and two types of phycoerythrin, PEI and 78 PEII, and are within the group of *Synechococcus* distinguishable by the presence of 79 chromophores phycoerythrobilin (PEB) and phycourobilin (PUB). PEB maximally absorbs light 80 in the range of 545 nm (green) and PUB maximally absorbs in the range of 495 nm (blue-green, 81 or cyan). In specialist strains, the ratio of PUB to PEB is fixed. Strains with high PUB:PEB are 82 herein referred to as blue-specialists, and low PUB:PEB as green-specialists. For CA4 83 generalists, the PUB:PEB ratio is variable. This variable PUB:PEB is controlled by groups of 84 genes within a genetic island, with two known variants, CA4-A and CA4-B (Humily et al., 2013). The combination of phycobiliproteins and chromophores result in the categorization of 85 Synechococcus into pigment types (PTs) denoted by numbers: PT1- PT3 for the added presence 86 of phycocyanin, PEI, and PEII, respectively (Six et al., 2007). PTs can be further classified into 87 88 smaller groupings. PT3, for example, is further divided based on relative chromophore ratios, 89 and is the only PT containing generalists. PT3a - 3d designate low, medium, high, and variable 90 ratios of PUB to PEB (PUB:PEB), and strains containing whole or partial CA4-A or CA4-B gene 91 islands are denoted with the suffix A or B. These groupings are continuously expanded and 92 updated to include slight variations on the general ones listed here (Humily et al., 2013; Xia et 93 al., 2018).

94 The ecological niches of marine *Synechococcus* are determined mainly by temperature, 95 and nutrient availability, but CA4 generalists exist across these ecological niches (Ahlgren et al., 96 2020; Ahlgren & Rocap, 2012; Farrant et al., 2016). Additionally, CA4-A and CA4-B strains 97 correlate with different environmental conditions (Grébert et al., 2018) making the reason for 98 evolutionary selection of CA4 difficult to identify. Given that CA4 is a spectral acclimation trait, 99 we may expect physical factors that influence the underwater color to also influence the ratio of 100 CA4 generalists to specialists. Since acclimation takes 4-6 days to complete (Humily et al., 2013; 101 Sanfilippo et al., 2016), variations with smaller timescales, such as cloud cover or light caustics, 102 can be ignored as key selection features for generalists (Stomp et al., 2008). On the contrary, 103 wind-driven mixing can change the light field for cyanobacteria within the mixed layer, moving 104 strains from wide spectrum surface waters to narrow spectrum deep waters that last throughout a 105 season. Areas prone to phytoplankton blooms, with high chlorophyll absorption at 440 nm, or 106 coccolithophore peak reflectance at 490 nm (Moore et al., 2012), also lead to underwater spectral 107 shifts that could select for generalists. The hypothesis that generalists may outcompete specialists 108 in areas with deep vertical mixing and/or high productivity has not been tested directly, but is 109 substantiated by the presence of higher abundances of generalists in regions that fit these 110 descriptions, such as the Chilean upwelling zone (Grébert et al., 2018).

111 Here, we explored the hypothesis that variations in the blue-green light field triggered by 112 physical mixing or changes in surface absorption (specifically, blue absorption by chlorophyll-113 dominated plankton) result in higher percentages of generalists in the Synechococcus population. 114 We first investigated the effects of the timing of blue-green color variation in a hypothetical 115 ocean water column (Stomp et al., 2007, 2008), where CA4 generalists and blue and green 116 specialists compete solely based on their different spectra of light absorption and light-harvesting 117 strategies. Blue-green variations produced in the model light field were forced by oscillating 118 between two light colors, with oscillation periods that varied to be faster, at the same rate, and 119 slower than the pace of acclimation. Then, more akin to open ocean conditions, we tested the 120 effect of various depths of the homogenous mixed layer, and concentrations of chlorophyll-121 dominated phytoplankton in daylight spectra. We compared model results to *in situ* data on the 122 proportion of Svnechococcus generalists in metagenomic datasets collated from seven global 123 ocean cruises as part of the biological initiative of the Global Ocean Ship-based Hydrographic 124 Investigations Program (Bio-GO-SHIP), supplemented with four cruises from GEOTRACES, 125 and over 150 stations from TARA Oceans. Our focus on the partitioning of the Synechococcus population allowed us to determine the specific drivers of high percentages of generalists relative 126 127 to specialists in the Svnechococcus population.

129 2. Materials and Methods

130 2.1 Competition model

131 We simulated the time evolution of growth of *Svnechococcus* PT3a (low PUB:PEB), 132 PT3c (high PUB:PEB), and PT3d (variable PUB:PEB) strains (cells/m3) acclimating to blue and 133 green light. This built on a previous study (Stomp et al., 2008) where three cyanobacteria 134 populations competed for light based on the available light spectrum, using model equations for 135 two fixed phenotypes and one flexible phenotype in red or green light as for CA3 strains. Each 136 population was distinguished by their specific absorption spectrum as displayed in Fig. 1. All 137 strains had equal maximum growth rates, p_{max} , photosynthetic efficiencies, φ , and loss rates, L 138 (Table S1). Light penetration through the model followed exponential decay with available light 139 at each depth layer influenced by absorption by seawater as well as the cyanobacteria 140 populations. In our version of the model, the depth of the water column was variable, and 141 additional absorption by chlorophyll and coccolithophores were added as options in addition to

142 the absorption by seawater.

143 The model solution yielded the relative abundance of the three cyanobacteria pigment 144 types integrated across the one-dimensional layer. Equilibrium was reached when light-limited 145 growth was equal to loss. The model variables explored for their impact on the Synechococcus competing populations were the depth of the model layer, z_m ; the incoming light spectra 146 147 (whether blue/green/cyan and timing of oscillations, or the spectrum of daylight); and 148 concentrations of chlorophyll or coccolithophores in the ambient water that affect light 149 absorption by the competing strains. Descriptions of the model equations required to reproduce the results are provided in Supplemental Text S1, and model code (in MATLAB version 9.7.0, 150

- 151 R2019b, MathWorks Inc.) is publicly available (Lovindeer, 2021).
- 152 2.1.1 Model environment & mixed layer depth

The model environment consisted of a one-dimensional aqueous layer of thickness, z_m , that was considered homogenous except for light penetration, which followed exponential decay by Beer-Lambert's law with depth. These conditions are similar to the dynamics of a well-mixed layer in the ocean, and z_m was considered synonymous with the mixed layer depth. The decay of light through the layer to z_m was calculated per wavelength at discrete depth intervals (Eqn. S3) and final results integrated from 0 to z_m . Simulations were made with various magnitudes of z_m , from 1 to 150 meters.

- Light absorption with depth and wavelength were functions of the absorption spectrum of seawater (Buiteveld et al., 1994); absorption spectrum of each *Synechococcus* strain (Fig. 1); and absorption spectra of added ocean water constituents (chlorophyll and coccolithophores),
- 163 concentrations of which were prescribed before each simulation (see 1.3 below). Each
- 164 Synechococcus strain within the model was treated as a continuous tracer with increased light
- absorption over time and scattering properties ignored. Growth stagnated, and equilibrium was

166 reached, when light penetrating the aqueous layer limited growth to be equal to the prescribed 167 loss rate (Eqn. S6).

168 No parameters for mixing or turbulence were included. Variability between light colors 169 that may occur during mixing were externally forced by oscillating input light colors in the blue-170 green region of the spectrum (see 2.1.2 below). The emission spectrum of daylight was used for 171 input light in all other simulations (2.1.3).

172 Time of oscillating light color 2.1.2

173 To simulate variability in light color that may occur in surface waters, oscillation between 174 blue, green, and cyan light spectra were used. Oscillations periods varied in timescale from faster

than acclimation times (< 1 day), at the same rate of acclimation (3 - 6 days) to beyond 175

176

acclimation time (> 10 days). Oscillations were created using a sine function, F, as a switch

177 between light colors (e.g. F > 0 blue, F < 0 green, Eqn. S8) with oscillation periods controlled by

178 a constant that resulted in five periods of 0.6, 3, 6, 11, and 31 days.

179 Incoming spectra for light colors (Fig. S1) were acquired from the emission spectra of

180 light emitting diodes (LEDs) in blue (PARsource), green (Illuminati), and cvan (Cvril

181 McCormick, University of California, Irvine), measured using an LI-180 spectrometer (LI-

182 COR). Blue LEDs had peak emission at 440 nm with shoulders ±30 nm consistent with the blue

183 light used to discover and subsequently document CA4 throughout the literature (Palenik, 2001;

184 Everroad et al., 2006; Six et al., 2007; Humily et al., 2013; Sanfilippo et al., 2016; Mahmoud et

185 al., 2017). Green LEDs had peak emission at 520 nm with shoulders ±40 nm. A cyan LED was

included to overlap the peak at 495 nm, but was not available commercially and was built from 186

187 diodes mounted to a copper board with heat sink. The resulting spectrum had higher emission at

188 495 nm but wide emission (430 - 620 nm). For comparison to a narrow emission band of cyan 189 light with peak at 495 nm, we created a spectrum in the model by mathematically shifting the

190 measured spectrum for the blue LED, with peak at 440 nm, to 495 nm.

191 Simulations with LED lights only included absorption from seawater and the competing 192 strains, with absorption by chlorophyll-a and coccolithophores set to 0.



194

195 **Figure. 1**: Relative absorption spectra measured for *Synechococcus* strains WH8102 (blue-

specialist), WH7803 (green-specialist), and WH8020 fully acclimated to green light (CA4 green-

acclimation) and to blue light (CA4 blue-acclimation). Absorption spectra have been normalizedto zero absorption at 700 nm.

199

200 2.1.3 Constant daylight with chlorophyll absorption

Simulations in constant daylight used the above-water spectrum (μ W cm⁻² nm⁻¹) measured from 400 – 700 nm by an optical profiler deployed at the surface in "buoy mode" on a TARA Mediterranean cruise in sunny conditions at 2pm on 26 Aug 2014 from 43.57 N, 7.33 W (seabass.gsfc.nasa.gov/experiment/Tara_Mediterranean). Units were converted to μ mol photons m⁻² s⁻¹ nm⁻¹ using a conversion factor from W m⁻² to photons of 4.57 (Sager & McFarlane, 1997). The resulting spectra is displayed in Fig. S1.

207 Chlorophyll-dominated phytoplankton were modeled using the specific absorption 208 spectrum of chlorophyll-*a*, which changed as a function of chlorophyll concentration(Bricaud et 209 al., 1995). Absorption of chlorophyll in the water column at each wavelength (m⁻¹) was 210 calculated by multiplying the specific absorption spectrum (m² mg⁻¹, Fig. S2) by the model's 211 prescribed chlorophyll concentration, which ranged from 0 - 20 mg m⁻³. Absorption by 212 coccolithophores was calculated similarly, using the specific absorption spectrum of *Emiliania* 213 *huxleyi* (Sadeghi et al., 2012) (m² mg⁻¹, Fig. S2) and concentrations from 0 - 20 mg m⁻³.

214 2.1.4 Model biology

215 Competing *Synechococcus* strains in the model were distinguishable by their specific 216 absorption spectra (Fig. 1). The rate of change for acclimation was determined by an acclimation 217 fraction, v, that was modified to increase PUB:PEB in ambient blue light and decrease PUB:PEB 218 in green light as described in Eqns. S1 – S2.

- 219 Growth of the strains over time was a function of their maximum growth rates, their
- photosynthetic efficiencies, and the quanta of light absorbed per wavelength by each strain from
- 400 700 nm (Eqn. S6). Parameters for growth were acquired from monoculture laboratory
 experiments with *Synechococcus* strains WH8102 (blue-specialist), WH7803 (green-specialist),
- and CA4 acclimaters RS9916 and WH8020, in nutrient replete conditions under blue, green, and
- white LED light (Table S1). The model was calibrated using input light emissions that matched
- the continuous LED lights used in experiments. Maximum growth rates (0.7 day⁻¹ in green light,
- 226 $p_{max,green}$, and 0.5 day⁻¹ in blue light, $p_{max,blue}$), photosynthetic efficiency (2.4 x 10⁶ cells
- 227 (µmol photons)⁻¹ in green light, φ_{green} , and 1.2 x 10⁶ cells (µmol photons)⁻¹ in blue light, φ_{blue}),
- and a prescribed loss rate of 0.005 hr^{-1} (L) were kept constant for all strains within the model.
- 229 This ensured that differences in growth were only attributable to differences in absorption
- 230 spectra. The concentration of each strain integrated across z_m was calculated per unit time.
- Abundances at model equilibrium were converted to percentages of the final population at
- equilibrium for comparison across model simulations.
- 233 2.2 *In* situ data

Available cruise data from campaigns in the Atlantic, Pacific and Indian Oceans from 2009 to 2018 were collated and used in this study. This included 11 cruise transects–Bio-GO-236 SHIP AE1319, NH1418, BV46, AMT28, IO9, IO7, P18, (Larkin et al., 2021) GEOTRACES 237 GA02, GA03, GA10 & GP13 (Biller et al., 2018; Schlitzer et al., 2018)–and 153 stations from 238 TARA Oceans (Picheral et al., 2014; Sunagawa et al., 2015). Correlation analyses were

239 performed on the proportion of generalists in the *Synechococcus* population. Analyses were

- 240 performed in MATLAB.
- 241 2.2.1 Metagenomic processing of cruise data

242 Raw metagenomic reads were quality controlled, and adapter sequences trimmed using Trimmomatic v0.35 (Bolger et al., 2014). Trimmed reads were recruited to a reference dataset of 243 115 genomes with representatives of each ecotype of Synechococcus, Prochlorococcus, and 244 245 *Pelagibacter* as well as a *Roseobacter* reference to help reduce false recruitment of closely related reads. Bowtie2 v2.2.7 (Langmead & Salzberg, 2012) was used for read recruitment with 246 the following flags: --no-unal --local -D 15 -R 2 -L 15 -N 1 --gbar 1 --mp 3. Resulting SAM files 247 were sorted and indexed into BAM files using samtools v1.3 (Li et al., 2009). Recruited reads 248 249 were then profiled using Anvi'o v5 (Eren et al., 2015). Genes were identified by aligning and 250 clustering all open reading frames in the reference dataset using NCBI BLAST (Altschul et al., 251 1990) and MCL (van Dongen & Abreu-Goodger, 2012) through the Anvi'o pangenomic 252 workflow (Delmont & Eren, 2018). The clusters were curated selecting genes of interest (Table 253 S2) and coverages were calculated using MATLAB scripts (version 9.5.0, R2018b; Ustick, 254 2021).

255 2.2.2 Estimation of pigment type abundances

The relative abundance of generalists (PTs 3d & 3e) and specialists (PTs 3a, 3b, 3c, & 3f) were calculated using the coverage of the genes *mpeAB* and *mpeW* matched to PTs (Grébert et al., 2018)(Table S2). Total PT abundance was estimated by normalizing coverages to raw read pair counts per sample. Samples with less than 5x total *mpeAB* coverage were removed from the analysis.

261 2.2.3 Assignment of pigment type for unknown genomes

262 To identify the pigment type of uncharacterized reference genomes, a phylogeny of the 263 mpeAB genes was created. The sequences were aligned using Mega7 (Kumar et al., 2016) and 264 Muscle (Edgar, 2004). Maximum likelihood fits of 24 different nucleotide substitution models 265 were estimated using MEGA7, and GTR+Gamma was selected due to low Bayesian Information 266 Criterion and Akaike Information Criterion values. A phylogenetic tree was generated using 267 raxml (Stamatakis, 2014) with the following arguments -T 6 -f a -x 123 -p 123 -N 1000 -m 268 GTRGAMMA -O. PT3 variants were assigned based on *mpeAB* sequence variation and also the 269 presence-absence of *mpeW* and *mpeZ* in the reference genome (Fig. S3). Resulting tree, bootstrap 270 values, and assignments were visualized using iTOL (Letunic & Bork, 2007).

271 2.3 Mixed layer depth (MLD) and temperature from cruise data

Data from cruise CTD profiles were downloaded for each cruise from publicly available repositories for GO-SHIP from https://cchdo.ucsd.edu accessed 13-Feb-2020, GEOTRACES intermediate data product 2017 version 1 from http://www.bodc.ac.uk/geotraces/data/idp2017 accessed 02-Oct-2020 (Schlitzer et al., 2018), and TARA Oceans stations 001 – 210 from http://oceans.taraexpeditions.org accessed 28-Oct-2020 (Picheral et al., 2014).

277 A range of methods exist in the literature for calculating mixed layer depth (de Boyer 278 Montégut, 2004; Holte & Talley, 2009) and MLD calculations were compared across these 279 methods using the methodology described in (Holte & Talley, 2009). A dataset for calculating 280 seawater density parameters used for MLD calculations (seawater ver3 3.1.zip downloaded on 281 02-Dec-2020) was provided by the Commonwealth Scientific and Industrial Research 282 Organisation (CSIRO) through a Creative Commons Attribution 4.0 International Licence. The 283 threshold method (de Boyer Montégut, 2004) with a temperature threshold of 0.2°C from a 284 surface reference of 10 m was used for this study, as this method aligned best with visually 285 inspected profiles from cruise CTD casts. Match-ups between calculated MLDs from CTD 286 profiles and the proportion of *Synechococcus* PTs yielded 629 points for correlation analyses. 287 The average temperature of the mixed layer was calculated by averaging all temperature values 288 between the 10 m reference depth and the mixed layer depth. Temperature values were reported 289 in the text \pm one standard deviation.

290 2.3 Mixed layer depth monthly climatology

291 Data on monthly mixed layer depth climatology (Holte et al., 2017) from the Global

Ocean Observing System Argo Program was downloaded in MATLAB format on 17-Sep-2020

from a public repository at the University of California, San Diego (<u>http://mixedlayer.ucsd.edu</u>).

- The dataset was used to create the climatological means from January 2000 to December 2019.
 Monthly mean mixed layer depth was retrieved for the month and grid sampling location of each
- *Synechococcus* genetic data point. A total of 605 co-located data points were used for analyses.
- 297 2.4 Sea Surface Height climatology and gradients

298 Monthly, binned, 1 degree gridded level 4 absolute dynamic topography / sea surface 299 height above the geoid (SSH, m) from October 1992 to December 2010 was retrieved on 29-

300 Dec-2020 from the Physical Oceanography Distributed Active Archive Center (PO.DAAC) at

301 NASA's Jet Propulsion Lab . The SSH dataset was derived from measurements by several

302 satellites (Envisat, TOPEX/Poseidon, Jason-1 and OSTM/Jason-2) and was provided by

Archiving, Validation, and Interpretation of Satellite Oceanographic Data (AVISO, 2011).

Values were averaged by month to obtain monthly climatology of SSH from 1992 – 2010. Co located values matching the month of sampling of each genetic data point was retrieved from the

306 dataset and yielded 569 matched values. SSH gradients were calculated using absolute

307 differences in SSH between nearest one-degree grid cells.

308 2.5 Statistical analyses

All statistical analyses were performed in MATLAB. Linear regression analyses were conducted for results of the model simulations and *in-situ* data correlations. Correlation analyses for *in situ* data were conducted between all physical oceanographic parameters and the percent of generalists in the *Synechococcus* population calculated as the combined read abundances of

313 PT3d over total *mpeAB* reads. Regression coefficients (\mathbb{R}^2), p-values (p), and the number of

314 samples for each analysis (n) are reported in the text or figure legends.

315

316 3. Results

317 *Conceptual model*

We modified a one-dimensional model of competition between cyanobacteria strains with different light-harvesting strategies and absorption spectra, based on equations in (Stomp et al., 2008), and tested the light-dependent factors driving the abundance of chromatic acclimating

321 generalists in the population. The model simulated the time evolution of growth (cells/m³) of

three strain populations that represented *Synechococcus* pigment types—a green-specialist PT3a,

a blue-specialist PT3c, and a generalist PT3d. We tested the effect of three variables on the

proportion of generalists in the resulting population at equilibrium. These were: 1) the timing of

325 oscillation between two light colors (blue/green, blue/cyan, cyan/green) which varied from faster

than acclimation (0.6 days), within the same pace of acclimation (3 - 6 days) and slower than acclimation (11 - 31 days); 2) depth of z_m (the homogenous layer); and 3) increasing chlorophyll-a and coccolithophore absorption in daylight.

329 The percentage of generalists in the *Synechococcus* population was determined primarily 330 by the depth of the homogenous layer ($R^2 = 0.73$, p < 0.001, n = 77; Fig. 2). For all simulations, 331 whether in LED light colors or in daylight, the percentage of generalists increased as z_m 332 increased (Fig. 2). Panels a – c in Figure 2 display an example at 3-day oscillation period with generalists dominating at $z_m > 10$ m. Similarly, in daylight (panels d – f) at constant 333 334 concentration of 0 and 15 mg m⁻³ chlorophyll-*a*/coccolithophore absorption, generalists 335 consistently dominated at deeper z_m , while green-specialists dominated at shallower z_m . 336 Absorption by chlorophyll-a and coccolithophores favored the green-specialist and increased the depth at which generalists dominated the population. For example, generalists were 100% of the 337

population at 80 m z_m in clear water (panel d) and 140 and 100 m z_m with 15 mg m⁻³ added chlorophyll-*a* and coccolithophore absorption, respectively (panels e and f).

340 We note that the acclimation fraction, v, that controls the extent of acclimation and ranges from fully acclimated to low PUB:PEB at v = 0 to fully acclimated to high PUB:PEB at 341 342 v = 1 remained at 0.4 in clear water simulations in daylight with $z_m >$, indicating an intermediate PUB:PEB acclimation range was maintained by the generalist strain. These 343 344 simulations were the only ones for which v did not equilibriate to 0 or 1. Chromatic acclimaters 345 have been shown to maintain intermediate PUB:PEB ranges when illuminated with different 346 ratios of blue and green light (Sanfilippo et al., 2016), such that the acclimation response is not 347 binary.

348 Oscillation time between light colors had no effect on the percentage of generalists in the 349 population. An example of the results at 1m depth and varying oscillation times is displayed in Fig. S4 panel a. The green-specialist dominated at 1 m z_m during blue/green, blue/cyan, and 350 351 cyan/green oscillations. That the green-specialist dominated during blue/cyan oscillations was 352 linked to the wide spectrum of the cyan LED used in the simulations. However, a much narrower 353 cyan spectrum with a distinct peak at 495 nm led to the blue specialist dominating (Fig. S4, panel 354 b). This indicates that the blue-specialist requires a narrow band of blue-shifted wavelengths 355 (between 440 – 495 nm) to dominate the population. A blue-dominance requirement for the blue-356 specialist was reinforced in daylight simulations, where the green-specialist dominated in clear 357 water (0 mg m⁻³ added chlorophyll or coccolithophore absorption). The spectrum of daylight 358 used in our simulations had a blue region spanning 450 - 500 nm that diminished more rapidly 359 with depth in comparison to the green region (500 - 550 nm) once competing strains were 360 present (Fig. S5). When the green-specialist was removed from the simulation, the bluespecialist dominated at 1 m z_m in daylight. Thus, the blue-specialist may only dominate in the 361 362 near absence of other strains, when the water column can maintain high ambient emission in the 363 blue region.



365

Figure. 2: Simulated population distribution at steady state equilibrium of *Synechococcus* generalist and specialists at various magnitudes of z_m . Panels **a** - **c** show results under continuous 3-day oscillation periods between two LED lights in the blue-green spectral region. Panels **d** - **f** show results under daylight with no additional pigment absorption (**d**) and absorption resulting from 15 mg m⁻³ added coccolithophores (**e**) and chlorophyll-*a* (**f**).

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With generalists only dominating at larger z_m , the results of our simulations suggest that the depth of the mixed layer is the main driver of the partitioning between *Synechococcus* generalists and specialists. As the model is a conceptual exploration into deterministic changes in the light field, it does not account for other factors that affect the distribution of *Synechococcus* in the ocean, such as nutrients and temperature (Zwirglmaier et al., 2008; Kent et al., 2019; Ahlgren et al., 2020). Thus, model results are confined to describing the light-dependent driver of the partitioning of the *Synechococcus* population.

380 Generalists in situ

381 To test whether mixed layer depth strongly selected for generalists *Synechococcus* strains 382 in the open ocean, we examined metagenomic data from 11 cruise transects (7 Bio-GO-SHIP and 383 4 GEOTRACES) along with 153 stations from TARA Oceans, for which concurrent conductivity, temperature and depth (CTD) profiles were available for mixed layer depth (MLD) 384 calculations. MLD was calculated using the method of (de Boyer Montégut, 2004) with a 385 386 temperature threshold of 0.2°C from a surface reference of 10 m, which worked best for the 387 profiles in our dataset. The Synechococcus population was identified using the mpeAB gene 388 marker mapped to PTs (Grébert et al., 2018) and generalists were defined as the combination of 389 PTs 3dA+3dB.

From global ocean cruise metagenomic data, *Synechococcus* had the highest percentage of generalists in high latitude regions above 30° north and south and within the Pacific equatorial upwelling zone (Fig. 3a).

393



394

Figure. 3: Global patterns of *Synechococcus* light-harvesting strategies and co-located sea
 surface height climatology. a) Percentage of *Synechococcus* CA4 acclimaters (pigment types

3dA+3dB) normalized to total *mpeAB* reads >5x total coverage from metagenomic datasets

between 2009-2018. b) Co-located monthly climatology of sea surface height (m) from 1992 -

- 399 2010 (569 points).
- 400

401 In contrast to the model simulations, MLD calculated from cruise data did not correlate 402 strongly with Synechococcus light-harvesting strategies. The percentage of generalists had low correlations with MLD calculated from CTD profiles across the dataset ($R^2 = 0.04$, n = 629, Fig. 403 404 4a). However, it is possible that point sampling of a CTD profile at oceanic stations does not 405 correlate well with the average MLD experienced at that station. For example, a mixed layer may 406 shoal on a particularly warm day of sampling in a region with an average deeper MLD. High 407 percentages of generalists along cruise tracks in similar areas but different sampling times (Fig. 408 3a) indicate possible adaptation to the mean state of ocean niche conditions. To account for a 409 possible mismatch in timescale between point sampling and the average MLD that the strains 410 may experience, we correlated the proportion of generalists with the climatological monthly 411 mean MLD from *in-situ* data generated by National Oceanic & Atmospheric Administration's 412 (NOAA) Global Ocean Monitoring & Observing autonomous Argo floats. CA4 strains had 413 higher positive correlations with monthly MLD climatology ($R^2 = 0.14$, n = 605, Fig 4b) 414 indicating that average MLD have a more significant role in the partitioning of Synechococcus

415 light-harvesting strategies.

416



Figure. 4: Scatter plot of the percentage of *Synechococcus* CA4 acclimaters correlated with colocated physical oceanographic properties. **a**) Mixed layer depth (MLD, m) from cruise CTD data retrieved from the same cruises as *Synechococcus* metagenomic samples ($R^2 = 0.04$, n = 629). **b**) Monthly mean MLD climatology from ARGO float data from Jan 2000 to Dec 2019 (R^2 = 0.14, n = 605). **c**) Monthly SSH climatology (m) from Oct 1992 to Dec 2010 satellite data (R^2 = 0.39, p < 0.001, n = 569). **d**) SSH absolute gradient (m) ($R^2 = 0.23$, p < 0.001, n = 560).

424

- 425 Much higher correlations were evident with the mean temperature of the mixed layer
- taken from cruise CTD data. Mixed layer average temperatures ranged from 9.6±0.1 °C to
- 427 31.2±0.2 °C. Generalists dominated at temperatures below 14°C and were significantly
- 428 anticorrelated with temperature across the dataset ($R^2 = 0.47$, p < 0.01, n = 629). The generalists
- 429 in our dataset were dominated by PT 3dA strains, found to be in high abundance in cold waters
- 430 (Grébert et al., 2018).

431 The distribution in Figure 3a indicates higher percentages of generalists in areas of major 432 ocean fronts, where cold and warm currents meet, which could provide significant energy for upper ocean turbulence (D'Asaro et al., 2011) not tested within our model. We investigated this 433 434 relationship using the climatological mean absolute dynamic topography, or sea surface height with respect to the geoid (SSH), as a remote sensing proxy for ocean fronts (Sun et al., 2011). 435 436 Using one-degree binned satellite data, we calculated gradients in SSH surface topography, as 437 higher gradients are indicative of oceanic frontal systems. CA4 strains positively correlated with 438 absolute SSH gradients ($R^2 = 0.23$, p < 0.01, n = 560, Fig 4c). Similar to correlations with 439 temperature, CA4 strains were highly correlated with low SSH ($R^2 = 0.39$, p < 0.001, n = 569,

- 440 Fig 4d).
- 441

442 **4. Discussion**

443 This study revealed that deep mixed layers, upwelling zones, and sea surface height 444 gradients, indicative of ocean fronts, are large-scale physical drivers of the partitioning between 445 Synechococcus light-harvesting generalists and specialists. Deep mixed layers in the model 446 environment with growing cyanobacteria strains reduced light availability in both blue and green 447 spectral regions over time (Fig. S5). The dominance of generalists with depth in the model could 448 reflect the benefit of their ability to manage an intermediate state in which there is equally strong 449 light absorption in both the blue and green spectral regions. Such was the case for the generalist 450 strain that maintained an intermediate PUB:PEB range (expressed as v = 0.4) in deep water. This 451 result indicates that in addition to environments for which generalists can fully acclimate to 452 either blue or green, a second, stable intermediate niche space exists for generalists, where light 453 can be available near equally in both 495 and 545 nm spectral regions. Such a stable intermediate 454 niche would only be applicable to phenotypic plasticity that is non-binary, as is the case for 455 chromatic acclimation.

A stable intermediate may also explain why light that varied faster than the acclimation time had no effect on the dominance of the generalists. Equal absorption at both 495 and 545 nm by the generalist was not evident during fast oscillation times in our model, but if the environment changed too rapidly, strains may acclimate to the average of the changing environment, which may be sensed as a static environment rather than a variable one. If that static environment is not the two end member colors, but rather a combination, a non-binary generalist may still be able to thrive. However, this idea is not supported by other non-binary

463 phenotypes for which timescales of variation have been shown to be important. Timescales faster 464 than the acclimation time modeled for the CA3 cyanobacteria strain Pseudanabaena CCY9509 465 did not favor the strain, and instead were too fast for the generalist to effectively outcompete 466 both green and red specialists (Stomp et al., 2008). Recent work (Walworth et al., 2020) has 467 shown that rapid fluctuations in physical environmental conditions that occur on timescales shorter than 10 microbial cell generations select for generalists (what the authors call low g-468 469 strategies), and prevent the evolution of specialists (high g-strategies), while stable environments 470 more quickly selected for specialists. Chromatic acclimation is completed within 6 microbial cell 471 generations (Everroad et al., 2006), and would benefit from such rapid fluctuations. Upwelling zones can transport water vertically at a rate of 12 m day⁻¹ and horizontally by 6 km day⁻¹ 472 473 (Tilstone et al., 2000), and could be considered rapid fluctuations. For Synechococcus strains 474 with average nutrient replete growth rates of 0.7 day⁻¹, vertical transport from deeper than 50 m 475 would align with acclimation times for generalists, driving their dominance in these environments. This is supported by other studies reporting high abundances of generalists in the 476 477 Synechococcus CRD1 and CRD2 clades that dominate the Costa Rica upwelling dome, as well CA4 strains in the Benguela upwelling, and the equatorial Pacific upwelling regions observed in 478 479 our dataset (Grébert et al., 2018; Sohm et al., 2016).

480 For deep mixing in the open ocean, vertical movement and turbulence create variability 481 for each individual strain that was not able to be replicated in our model. Deep mixed layers also 482 introduce more limiting light environments if mixing goes deeper than the euphotic zone depth, 483 which varies spatially as a function of chlorophyll from less than 10 m to greater than 80 m (Lee 484 et al., 2007). These factors could explain the large disparity between modeled and *in-situ* 485 correlations of generalists with MLD. A useful expansion to the current model may include 486 vertical exchange of phytoplankton with the inclusion of mixed layer diffusivity to examine the 487 spread of strains throughout the layer and calculate their ambient spectra with time. As mixed 488 layer diffusivity changes with seasons (Cronin et al., 2015), annual variability in diffusivity as 489 well as depth of the mixed layer and euphotic zone could be modeled in tandem. This would 490 provide useful information about how the proportion of light-harvesting strategies within the 491 Synechococcus community changes throughout seasonal cycles, and may explain the 492 climatological mean observations presented here.

493 The stark gradient of light harvesting strategies across temperature and sea surface height 494 indicate an important role of currents in the partitioning of Synechococcus strains. Ocean fronts 495 can cause re-stratification of the upper surface water, decreasing the MLD (Taylor & Ferrari, 496 2011) on a timescale of days (Mahadevan et al., 2010) and forming an independent selection 497 pressure for generalists in shallower MLDs. Though many studies have focused on nutrient and 498 light interactions for phytoplankton production at ocean fronts (Lima, 2002; Mahadevan, 2016), 499 no studies have resolved the impact of turbulence on the spectrum of visible light with depth in 500 these regions. As nutrient-light interactions within ocean fronts trigger phytoplankton blooms 501 (Taylor & Ferrari, 2011), we might expect a compounding effect of ocean water and chlorophyll 502 absorption on variation in the blue-green spectral region in these areas. Future studies in this area

- 503 could expand the one-dimensional model explored here to include episodic exchange between
- 504 deep and shallow mixing depths and explore the time variability of mixing, turbulence, and
- 505 blooms that could more readily lead to the selection of generalists we observe in the ocean.
- 506 General studies of the picoplanktonic composition of ocean fronts are also lacking. Most studies
- 507 on phytoplankton at ocean fronts focus on the movement of nutrients and the resulting
- 508 chlorophyll-dominated blooms observable by satellite (for example d'Ovidio et al., 2010;
- 509 Mahadevan, 2016). There is less focus on the effect of turbulence on the underwater spectrum, or
- 510 the picoplanktonic community that can result from changes in that light spectrum, leaving this
- 511 potential niche of *Synechococcus* generalists critically understudied.
- 512 Horizontal advection by ocean currents has been shown to affect the distribution of 513 phytoplankton niches *in situ* (d'Ovidio et al., 2010), becoming conduits for transfer of plankton, 514 potentially outside their preferred niches. Though horizontal advection was not modeled in our 515 study, we expect that specialists that have been horizontally transferred beyond their tolerances 516 for light, nutrients or temperature would not readily survive, while generalists, with wider
- 517 tolerances, may continue to thrive during advection. As such, horizontal advection could provide
- another physical oceanographic selection pressure for generalists that requires further study.
- 519 Together, physical ocean mixing contributes strongly to the partitioning of light-
- harvesting strategies in the *Synechococcus* population. In addition to nutrient kinetics known to
- 521 trigger phytoplankton blooms, wavelength acclimation may play a significant role in ocean
- frontal zones and upwelling areas. Thus, in addition to static ocean niches, dynamic ocean niches
- 523 seemingly impose their own selection pressure on the phytoplankton community structure,
- selecting for flexible light color harvesting phenotypes.
- 525

526 **5.** Conclusions

527 Physical mixing of ocean water is a selection pressure for the generalist light-harvesting strategy of chromatic acclimation in marine *Synechococcus*. High proportions of chromatic 528 529 acclimaters within the Synechococcus population were positively correlated with deep mixed layers, low sea surface temperature, low sea surface height, and large sea surface height 530 531 gradients in areas of major ocean currents. Climatological means of these ocean variables were 532 yielded higher correlations, indicating a possible adaptation of acclimaters to the mean state of 533 mixing present in upwelling zones and ocean fronts. This study indicates that ocean niches with 534 large-scale vertical movement and surface turbulence offer a substantial selection pressure within 535 the phytoplankton, and helps to explain the wide diversity of photosynthetic pigment strategies within marine Synechococcus, one of the most ubiquitous cyanobacteria in the ocean. 536

537

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- 549 <u>http://mixedlayer.ucsd.edu</u>); Bio-GO-SHIP metagenomes (<u>https://doi:10.1038/s41597-021-</u>
- 550 <u>00889-9</u>) and GO-SHIP vertical profiles (<u>https://cchdo.ucsd.edu/search?q=GO-SHIP</u>),
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- vertical profiles calculated from IDP 2017 (<u>https://doi.org/10.1016/j.chemgeo.2018.05.040</u>);
- 553 TARA Oceans metagenomes (<u>https://doi.org/10.1126/science.1261359</u>), and TARA Oceans
- vertical profiles (<u>https://doi.org/10.1594/PANGAEA.836321</u>), combinedly used to calculate the
- 555 proportion of *Synechococcus* pigment types in situ, and mixed layer depths, respectively.
- 556

557 Conflict of Interest

- 558 The authors declare no conflicts of interest
- 559

560 Data availability

- All datasets generated from this research are publicly available. Model code used to generate the
- 562 light color competition simulations is available at <u>https://doi.org/10.5281/ZENODO.4663350</u>,
- 563 with the resulting dataset at <u>https://doi.org/10.7280/D16688</u>. MATLAB scripts used to identify
- 564 *Synechococcus* gene coverage is available at <u>https://doi.org/10.5281/zenodo.4677447</u>. The
- 565 resulting *in situ* dataset of co-located *Synechococcus* pigment types and physical oceanographic
- 566 parameters of mixed layer depth, mixed layer depth properties (temperature, salinity, and
- density) and climatology, sea surface height, and sea surface gradients is available at
- 568 <u>https://doi.org/10.7280/D1XQ2P.</u>
- 569

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Supporting Information for

Upper Ocean Dynamics Select for Synechococcus Light Color Generalists

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Introduction

This supplement describes the model equations and parameters used in this study.

Text S1.

Model equations. Equations describing the model environment, taken from (Stomp et al., 2008) were modified for type IV chromatic acclimation as described below. Table S1 includes a list of model parameters and, where appropriate, their values.

The specific absorption spectrum of the chromatic acclimater strain $(k_{acclimator})$ was determined by the acclimation fraction, v, which varied between 0 - 1, and the specific absorption spectrum of the acclimator strain measured in blue light $(k_{acclimater,blue})$ and green light $(k_{acclimater,green})$ as calculated in Eqn. S1 and displayed in Fig. S1

$$k_{acclimater}(\lambda) = vk_{acclimater,blue}(\lambda) + (1 - v)k_{acclimater,green}(\lambda)$$
(S1)

where λ is the wavelength of light.

Change in v over time (Eqn. S2) is a function of the time taken to acclimate, controlled by a CA4 parameter α_c which is dependent on light color (subscript c), and the photons absorbed by the acclimater strain, $\gamma_{acclimater}$ (see Eqn. S7 below)

$$\frac{dv}{dt} = \alpha_c \frac{\varphi_c}{z_m} \int_0^{z_m} \frac{\delta \gamma_{acclimater}(z,v)}{\delta v} dz$$
(S2)

where z is size of one depth layer, z_m is the maximum depth of the mixed layer, and φ_c is the photosynthetic efficiency at each light color (subscript c), which is constant among strains.

Light penetrating the ocean at each wavelength and depth is a function of the incoming light spectrum at the ocean surface, I_{in} ; the specific absorption by each *Synechococcus* strain k_i , where i represents each strain; the cell abundance of each strain N_i ; the absorption by water a_w ; and the absorption by other plankton, a_{other} , where a_{other} was either 0, absorption by chlorophyll-a (a_{CHL}), or absorption by coccolithophores (a_{Coccos}) as described in Eqns. S3 – S5 below:

$$I(\lambda, z) = I_{in} \exp(-(\sum_{i=1}^{n} k_i(\lambda)N_i + a_w(\lambda) + a_{other}(\lambda))z)$$
(S3)

with

$$a_{CHL}(\lambda) = [CHL] (A_{CHL}(\lambda) ([CHL]^{-B_{CHL}})),$$
(S4)

$$a_{coccos}(\lambda) = [\text{coccolithophores}] (k_{coccos}), \tag{S5}$$

with the quantities in square brackets representing concentrations.

Change in the abundance of the *Synechococcus* strains with time, $\frac{dN_i}{dt}$ (Eqn S6) is given by the difference between cell loss and growth, where growth was a function of the photosynthetic efficiencies φ_i , and the number of photons absorbed by each strain at each depth interval $\gamma_i(z)$ – a match between the strain's specific absorption spectrum k_i , and the available light (Eqn. S7). Equations S6 and S7 are unmodified from the original formulation of Stomp et al., (2008):

$$\frac{dN_i}{dt} = \left[\frac{1}{z_m} \int_0^{z_m} \frac{p_{max,c} \gamma_i(z)}{\frac{p_{max,c}}{\varphi_i} + \gamma_i(z)} dz\right] N_i - LN_i$$
(S6)

$$\gamma_i(z) = \int_{400}^{700} I(\lambda, z) k_i(\lambda) d\lambda$$
(S7)

where $p_{max,c}$ is the maximum growth rate in each light color, which is a constant among strains, and *L* is the specific loss rate constant.

Oscillation between incoming light colors (e.g. blue and green) with time, t, in the model was controlled by a switch, F (S8), with F > 0 resulting in one color (e.g. blue) and F < 0 resulting in the other color (e.g. green) using an IF WHEN statement. The oscillation period was determined by A, where A values of 5, 1, 0.5, 0.3 and 0.1 resulted in corresponding oscillation periods of 0.6, 3, 6, 11, and 31 days, respectively.

 $F = \sin(At)$

(S8)



Figure S1. Peak normalized emission spectra of blue (PARsource), green (Illuminati) and cyan (Cyril McCormick, University of California, Irvine) LED lights measured using an LI-180 spectrometer (LI-COR) and the above-water spectrum of daylight measured in sunny conditions in the Mediterranean and adjusted to a surface PAR-integrated intensity of 1000 µmol photons m⁻² s⁻¹.



Figure S2. Representative graphs of the specific absorption spectra (m² mg⁻¹) of chlorophyll-*a* (the result of $(A_{CHL}(\lambda) ([CHL]^{-B_{CHL}}))$ in Eqn. S4 with $[CHL] = 10 \text{ mg m}^{-3}$) and for the coccolithophore *E. huxleyi* (k_{coccos} , Eqn. S5) used to calculate phytoplankton absorption in the model.



Figure S3. Phylogenetic tree rooted in *mpeAB* and showing the partition of *Synechococcus* pigment types into specialists (3a, 3c, 3cA, 3f) and generalists (3dA and 3dB). 3c strains were separated from 3dB strains by subtraction using the gene *mpeW* which is only present in 3dB strains. Previously unknown or unconfirmed pigment types that were assigned in this study are indicated with * and highlighted in pink.



Figure S4. Comparison of model results across oscillation periods between LED light colors that include cyan light with a wide (a) and narrow (b) spectral emissions at 1 m depth. Inserts at the top of panels a and b indicate the emission spectra of LED lights used to generate the results for each panel with the wide cyan spectrum spanning 430 - 620 nm with two emission peaks around 446 and 515 nm, and the narrow spectrum having one emission peak at 495 nm with shoulders ± 30 nm.



Figure S5. Penetration of the daylight spectrum through the model calculated at discrete depth layers, with each depth layer represented by a spectral line. No additional absorption by chlorophyll-dominated plankton was included. a) Light penetration at the beginning of the simulation (time, t = 0 days) with low abundance of *Synechococcus* strains and high background absorption by water. b) Light penetration during the simulation (t = 10 days) when the concentration of all three *Synechococcus* strains has increased and their absorption has decreased the relative availability of light from 440 – 500 nm compared to 500 – 550 nm at depth.

PARAMETERS	SYMBOL	UNIT	VALUE	REFERENCE
		mol photons m ⁻² s ⁻		
Incident Light Spectrum	I _{in}	¹ nm ⁻¹	Fig S1	measured
PAR-integrated incident light		mol photons m ⁻² s ⁻		
intensity, daylight		1	1000	measured
Specific absorption of			Fig. 1, Eqn	
Synechococcus strains	k _i	m^{-1} cell ⁻¹ nm^{-1}	S1	measured
Background seawater				(Buiteveld et al.,
absorption	a _w	$m^{-1} nm^{-1}$		1994)
			Fig. S2,	(Bricaud et al.,
Chlorophyll absorption	a _{CHL}	m ⁻¹ nm ⁻¹	Eqn S4	1995)
			Fig. 2S,	(Sadeghi et al.,
Coccolithophore absorption	a _{Coccos}	m ⁻¹ nm ⁻¹	Eqn S5	2012)
Specific loss rate	L	hr ⁻¹	0.005	
Max specific growth rate,				
green, white	$p_{max,green}$	day-1	0.7	measured
Max specific growth rate, blue	$p_{max,blue}$	day ⁻¹	0.5	measured
Photosynthetic efficiency,		cells (mol		
green, white	φ_{green}	photons) ⁻¹	2.4 x 10 ⁶	measured
		cells (mol		
Photosynthetic efficiency, blue	φ_{blue}	photons) ⁻¹	1.2 x 10 ⁶	measured
				Tuned in the
CA4 parameter, green	α_{green}	dimensionless	0.70	model
				Tuned in the
CA parameter, blue	α_{blue}	dimensionless	0.95	model

Table S1. Parameters for the light color competition model between *Synechococcus* blue and green-light specialist strains and type IV chromatic acclimater (CA4 generalist).

Classification	Phenotypic description	Pigment Type	CA4 genetic island	Marker genes
Target marine Synechococcus group	Contains both phycoerythrin I and phycoerythrin II which bind chromophores PUB and PEB	3	n/a	mpeAB
Specialists	low PUB	3a	n/a	mpeAB
	mid PUB	3b	n/a	mpeAB
	high PUB	3c	n/a	mpeAB - mpeW
	high PUB with slightly different gene composition from 3c	3f	n/a	mpeAB
Generalists	variable PUB	3dA	CA4-A	mpeAB
		3dB	CA4-B	mpeAB + mpeW
	variable PUB but smaller degree of variation	3eA / 3eB	CA4-A / B	mpeAB

Table S2. Description of genetic markers used to differentiate *Synechococcus* specialists and generalists in cruise metagenomic data taken from (Humily et al., 2014).