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Irradiance modulates thermal niche in a previously undescribed low-light and cold-adapted nano-diatom

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Abstract

Diatoms have well-recognized roles in fixing and exporting carbon and supplying energy to marine ecosystems, but only recently have we begun to explore the diversity and importance of nano- and pico-diatoms. Here, we describe a small (ca. 5 μm) diatom from the genus *Chaetoceros* isolated from a wintertime temperate estuary (2°C, Narragansett Bay, Rhode Island), with a unique obligate specialization for low-light environments (< 120 μmol photons m^{-2} s^{-1}). This diatom exhibits a striking interaction between irradiance and thermal responses whereby as temperatures increase, so does its susceptibility to light stress. Historical 18S rRNA amplicon data from our study site show this isolate was abundant throughout a 6-yr period, and its presence strongly correlates with winter and early spring months when light and temperature are low. Two amplicon sequence variants matching this isolate had a circumpolar distribution in Tara Polar Ocean Circle samples, indicating its unusual light and temperature requirements are adaptations to life in a cold, dark environment. We expect this isolate's low light, psychrophilic niche to shrink as future warming-induced stratification increases both light and temperature levels experienced by high latitude marine phytoplankton.

Photosynthesis by marine phytoplankton is responsible for 50% of the global net primary production. These photosynthetic protists also perform multiple ecosystem services (Lyle 1988; Smith and Hollibaugh 1993; Field et al. 1998), making them essential to study in the context of global climate change (Hutchins et al. 2019). Current projections suggest a rise in mean sea surface-water temperature of 4°C by 2100 (Pachauri et al. 2014) which could have large impacts on the physiology and composition of these microbial photosynthetic communities, and their ability to sequester carbon (Hutchins and Fu 2017). However, making predictions about warming effects on phytoplankton can be difficult, because of their still relatively underexplored biological diversity. This is especially true of small (< 5 μm) nano- and picoplankton, which prior to the advent of next-generation sequencing have been routinely under-sampled by microscopic techniques (Abad et al. 2016; Leblanc et al. 2018). For example, the smallest known diatom genus (*Minidiscus*) was recently shown to be capable of forming dense blooms, and similar very small diatom groups are now recognized as being globally abundant (Leblanc et al. 2018).

Although our knowledge of phytoplankton diversity is expanding, it is an open question how much functional thermal diversity exists within this observed phylogenetic diversity. For instance, phytoplankton communities can typically sustain growth well beyond current mean temperatures (Thomas et al. 2012). However, excursions above historical thermal maximum thresholds can cause major community restructuring (Kling et al. 2019), and so affect biogeochemistry (Hare et al. 2007; Feng et al. 2008). Lineage-specific predictions of temperature responses have often been based on just a handful of cultured model isolates, such as the diatom *Thalassiosira pseudonana* (Berges et al. 2002), the coccolithophore *Emiliania huxleyi* (Feng et al. 2008), and the diazotrophic cyanobacterium *Trichodesmium erythraeum* (Mulholland and Bernhardt 2005; Fu et al. 2014). However, the model organism approach to understanding resilience to rising temperatures in marine phytoplankton undoubtedly under-samples the potential range of thermal responses. Furthermore, lab-derived growth rates and other proxies for fitness can be uncertain predictors of ecological success. In situ, multiple environmental parameters (temperature, light, nutrients, and interspecific interactions such as competitive or trophic interactions) can vary simultaneously and have unexpected interactive effects on fitness (Jiang et al. 2018).

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In this study, we expand our knowledge of nanoplankton diversity by characterizing a previously unrecognized nanodiatom from a temperate estuary belonging to the genus *Chaetoceros*. In doing so, we demonstrate a unique interaction between temperature and light which together define its thermal niche. Combining lab-based physiology measurements with a wealth of taxonomic and ecological time series data spanning 6 yr and its global distribution in the Tara Oceans Dataset, we show this *Chaetoceros* is an abundant and widespread wintertime specialist. Further, we hypothesize its adaptations to both low-light and temperature make it vulnerable to the warmer conditions expected at mid- and high-latitudes with continuing climate change.

Methods

Isolation and culturing

The diatom investigated here was isolated from water collected at the Narragansett Bay Time Series (Rynearson et al. 2020) site (latitude 41.47, longitude −71.40) in March 2018. Surface-water temperature was 2°C at the time of collection. Collected water was prefiltered through a 100 μm mesh to remove large grazers, and then sorted at the University of Rhode Island Graduate School of Oceanography using a BD Influx flow cytometer (San Jose, California, U.S.A.). Cells approximately 5 μm and smaller with chlorophyll *a* (Chl *a*) fluorescence were sorted into 96 well plates containing natural seawater amended with nutrients following the recipe for F media diluted to F/20 (Guillard 1975). Wells showing positive growth over time were transferred to new media while gradually increasing nutrients to F/2 concentrations in Aquil artificial seawater (Sunda et al. 2005). Both initial isolates and stock cultures were maintained at 4°C and 30 μmol photons m^{-2} s^{-1} of cool-white fluorescent light on a 12 : 12 light : dark cycle (this was the day length in Narragansett Bay at the time of isolation), and diluted biweekly with fresh medium. Several dozen morphologically identical strains were collected, all with an apparent sensitivity to light (inability to grow at 150 μmol photons m^{-2} s^{-1}, data not shown). A single isolate strain was selected arbitrarily and used for all subsequent experiments.

Temperature and light assays

All culture work was done in climate controlled walk-in incubators under cool white fluorescent lights. Light levels were verified with daily measurements using a LI-250A spherical light meter (LI-COR Biosciences, Lincoln, Nebraska, USA). Cultures were kept in triplicate 15-mL polystyrene culture vials, and temperatures for all experiments were set using a series of water baths, each with its own thermostat, heater, and cooling element. Replicates were kept in exponential phase by diluting cultures with sterile medium when biomass reached a predetermined threshold. Cultures were acclimated to each combination of irradiance (15, 30, 50, 60, 70, 100, and 120 μmol photons m^{-2} s^{-1}) and temperature (2°C, 8°C, 12°C, 14°C, 16°C, 18°C, 20°C, 22°C, 24°C, 26°C) for 2 weeks.

After acclimation, growth rates were determined daily using in vivo fluorescence on a Turner AU-10 fluorometer (Turner Designs, Sunnyvale, California, U.S.A.) for an additional 7–10 d. In vivo fluorescence was used as a proxy for photosynthetic biomass because it allowed efficient daily measurements of a large number of simultaneously maintained cultures (as many as 90 at a time). All well-acclimated replicates were kept in the same nutrient conditions and growth rates were calculated from in vivo fluorescence of each individual replicate measured relative to itself over time (Gilstad and Sakshaug 1990; Wood et al. 2005; Kling et al. 2019).

Specific growth rates were calculated with the GrowthTools R package (DOI:10.5281/zenodo.3634918) using the slope of a regression line fit to the log of these data (Wood et al. 2005). Growth rates for cultures acclimated to 16°C were calculated for seven light intensities. In addition, we measured growth rates vs. each temperature in cultures acclimated to irradiances of 15, 30, or 50 μmol photons m^{-2} s^{-1}. GrowthTools (DOI:10.5281/zenodo.3634918) was used again to calculate thermal performance curves using the Eppley-Norberg model (Norberg 2004; Thomas et al. 2012). For the thermal curve done under 15 μmol photons m^{-2} s^{-1}, 4°C was used as the lowest temperature instead of 2°C.

In addition to acclimated growth experiments, we exposed the cultures to short-term doses of extreme light levels on the order of hundreds of μmol photons m^{-2} s^{-1}, similar to published diatom light-stress experiments (Zhu and Green 2010; Dong et al. 2016). For these experiments, we used ca. 638 μmol photons m^{-2} s^{-1}, which approximated the highest value measured during the 50-yr data set of surface irradiance from the Narragansett Bay Time Series (https://web.uri.edu/gso/research/plankton/data/). It is important to note that these measurements were mostly taken early in the morning and actually daily irradiance maximums measured at nearby station NARPCMET can be as high as 1700 μmol photons m^{-2} s^{-1} (https://cdmo.baruch.sc.edu/dges/). Triplicate cultures acclimated to either 4°C or 16°C and 30 μmol photons m^{-2} s^{-1} were exposed to this extreme light level for 1, 3, or 6 h, and compared to triplicate cultures that were not exposed (negative control), or were continuously exposed (positive control). After the exposure period, cultures were moved back to 30 μmol photons m^{-2} s^{-1} and fluorescence were recorded twice daily over 3 d of a 12 : 12 h light : dark cycle.

Sequencing

For sequencing, 200 mL of dense culture was filtered onto a 0.22 μm polyethersulfone Whatman Nucleopore filter (GE Healthcare, Chicago, Illinois, U.S.A.) flash frozen with liquid nitrogen and stored at −80°C. DNA were extracted using a DNEasy Power Water kit (Qiagen, German Town, Maryland, U.S.A.), and prepared for sequencing using the Nextera DNA Flex Library Prep kit (Illumina, San Diego,

California, U.S.A.). Sequencing was done at the University of Southern California's Genome Core on a Illumina Nextseq 550. Raw sequence data were quality checked using Fastqc (https://www.bioinformatics.babraham.ac.uk/projects/fastqc/, v. 0.11.8) and Multiqc (Ewels et al. 2016, v. 1.6) and low quality bases were removed with Trimmomatic (Bolger et al. 2014, v. 0.38). To recover 18S rRNA gene sequences, we used Bowtie2 (Langmead and Salzberg 2012, v. 2.3.5) to map all reads to a data set of 200 complete or nearly complete (> 1000 bp) *Chaetoceros* 18S rRNA gene sequences downloaded from NCBI. Reads that mapped even once were recovered using Seqtk (https://github.com/lh3/seqtk, v. 1.3) and assembled with SPAdes (Bankevich et al. 2012, v. 3.11). To identify our isolate, full length copies of the 18S rRNA gene sequence were downloaded from NCBI for 25 distinctly named species of *Chaetoceros*. The pennate diatom *Pseudo-nitzschia australis* was included as an outgroup. All sequences were aligned using Muscle (Edgar 2004, v. 3.8.31), the alignment was trimmed using trimAL (Capella-Gutiérrez et al. 2009, v. 1.4.15), and FastTree (Price et al. 2009, v. 2.1.10) was used to construct a phylogenetic tree.

Six years of amplicon sequencing data from our study site using diatom-specific primers matching the V4 hypervariable region of the 18S rRNA gene (Zimmermann et al. 2011) were obtained from Rynearson et al. 2020. Raw sequence data were downloaded from NCBI (PRJNA327394) and quality filtered as for the Illumina sequencing. Quality-controlled reads were merged and denoised into amplicon sequence variants (ASVs) using DADA2 (Callahan et al. 2016, v. 1.14.0). BLAST (McGinnis and Madden 2004, v. 2.9.0) was used to identify ASVs that matched the V4 rRNA gene sequence from the full length sequence assembled from our genomic data.

We also mined years of observational data to put the occurrence of our isolate ASV in Narragansett Bay into a long-term temperature and irradiance context. Records of surface-water temperature data matching the amplicon sequencing data were downloaded from the Narragansett Bay Time-series website (https://web.uri.edu/gso/research/plankton/data/). Dates without water temperature measurements from the time-series data set were supplemented by surface-water temperature data from the National Data Buoy Centers station QPTR1–8454049 at nearby Quonset Point (https://www.ndbc.noaa.gov/station_page.php?station=qptr1). Irradiance data for Narragansett Bay were downloaded from the National Research Reserve System's Central Data Management Office website (https://cdmo.baruch.sc.edu/dges/) for station NARPCMET. To account for the changing amount of irradiance experienced by phytoplankton due to variations in day length and weather, these data were converted from instantaneous irradiance (μmol photons m^{-2} s^{-1}) to total irradiance at the water's surface during a day (moles photons m^{-2} d^{-1}). To avoid over-inflating potential correlations between changing relative abundance within the diatom community (caused by differences in 18S rRNA gene copy number) and environmental factors, we used 1% relative abundance as a threshold and calculated the changing probability of an observation being above this threshold under different conditions. For instance, if our diatom had a relative abundance > 1% in half of a group of samples then its probability of detection was 0.5.

We utilized the Tara Oceans V9 amplicon data set (De Vargas et al. 2015) to understand the distribution of this isolate beyond Narragansett Bay. Sequence data from low- and mid-latitudes previously analyzed and resolved into ASVs

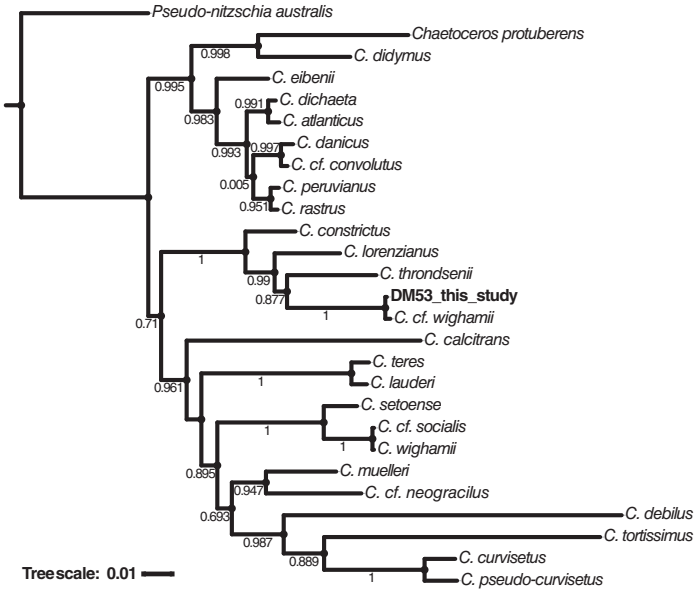

Fig 1. Phylogenetic tree representing the diversity of the diatom genus *Chaetoceros* constructed using full-length 18S rRNA gene sequences from NCBI. A sequence from the pennate diatom *Pseudo-nitzschia australis* is included as an outgroup. The isolate described in this study, DM53, is highlighted in bold.

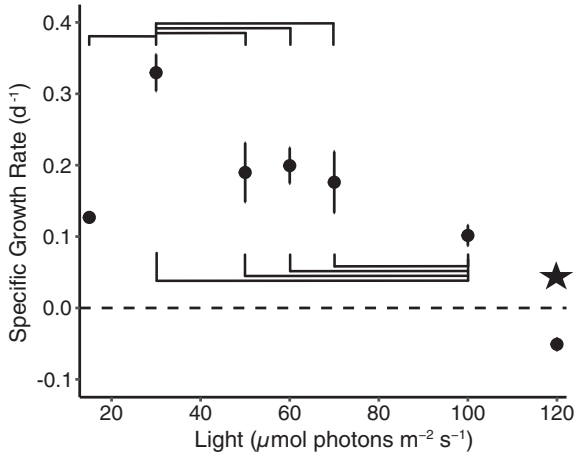

Fig 2. Growth rates at 16 °C across a range of seven light intensities for our Chaetoceros sp. isolate. Error bars represent ±1 standard deviation. Stars show treatments that are statistically significant ($p < 0.05$) compared to all other treatments via Tukey's test following a one-way ANOVA. Brackets indicate statistical significance between specific samples.

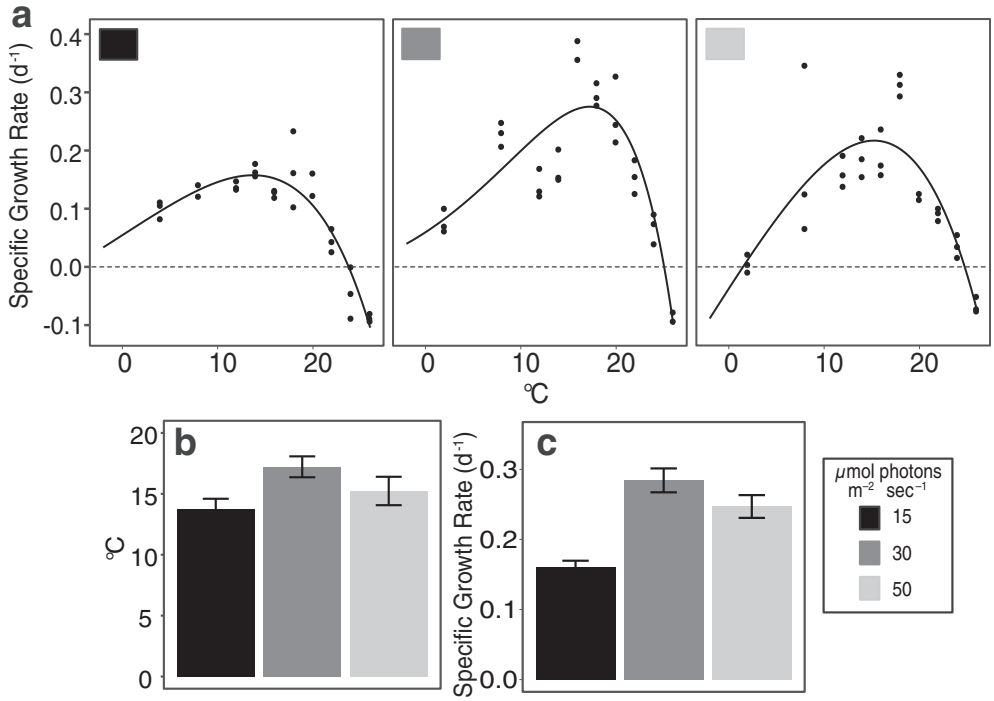

Fig 3. a) Thermal performance curves across three light levels. For all Eppley-Norberg curves, $r^2 > 0.7$ and all are significantly different from each other using repeated measure ANOVA ($p < 0.001$). Dashed horizontal lines show zero growth. Differences between light treatments are shown for the **b)** thermal optimum (Topt) and **c)** maximum growth rate (μMax). Error bars show ±1 standard deviation within the modelled optimal temperatures and maximum growth rates for each.

using DADA2 were screened for the presence of this isolate diatom using BLAST (McGinnis and Madden 2004; Callahan et al. 2017). In addition, we downloaded the Tara Polar data set and analyzed all amplicon sequencing data for these Arctic Ocean surface samples collected on filters with a pore size < 5 μm. Reads were denoised following the published script in Callahan et al. (2017).

Statistics and data availability

All statistics for analyzing these data and graphic visualizations were done using R (R Core Team 2019, v. 3.6.1) and Rstudio (Rstudio Team 2020, v. 1.13.83). Differences between light treatments were determined using a one-way ANOVA and the Tukey test, while differences between thermal performance curves were assessed using a repeated measure ANOVA. In both cases, significance was determined at the $p < 0.05$ level. All environmental data compiled in this study, the output from DADA2, scripts used to download the Tara Polar Ocean Circle samples, and scripts used in analysis have been made publicly available at https://figshare.com/projects/nanodiatom_temp_light/74283. Sequence data can be found on NCBI under the SRA accession PRJNA608686 (raw Illumina reads) and MT742785 (assembled 18S rRNA sequence).

Results

Taxonomy

Short read sequencing produced 9 million 150 bp paired-end Illumina reads. Mapping reads to 200 full length *Chaetoceros* spp. 18S sequences and assembling all mapped reads produced a single contig 1812 bp long. When BLASTed against the nt database, excluding all noncultured isolates, this assembled 18S rRNA gene sequence was the closest match to *C. cf. wighamii* strain BH65_48, with 99.8% identity across 92% of the sequence (accession KY980353.1). Unfortunately, isolation information was not available for this strain. However, the next closest match was to another *C. cf. wighamii* strain from the Roscoff Culture Collection (RCC3008, KT860959.1) at 100% identity across 90% of the query. This strain was isolated from the coastal Baltic Sea in 2010 at 4°C and was maintained at 50 μmol photons m^{-2} s^{-1}, similar to our isolate. Aligning 25 full length 18S sequences for named *Chaetoceros* species (Supporting Information Table S1) allowed us to construct a high quality phylogenetic tree (average maximum likelihood = 0.91) of this genus (Fig. 1). The next closest branching sequence was to other temperate isolates: *C. throndsenii* from the Gulf of Naples (93.6% ID and 96% coverage), *C. lorenzianus* (94.1% ID and 90% coverage),

C. constrictus (93% ID and 94.3% coverage) from Las Cruces, Chile.

Light curve

When grown at 16°C, this diatom isolate had an asymmetric response to increasing light levels, skewed toward low irradiance (Fig. 2). Although at the lowest light level tested (15 μmol photons m^{-2} s^{-1}) the specific growth rate was only 0.13 d^{-1} ($\pm$ 0.01), when irradiance was increased to 30 μmol photons m^{-2} s^{-1}, the growth rate nearly tripled, to 0.33 d^{-1} ($\pm$ 0.03). At this light level, the specific growth rate was significantly higher than at every other irradiance level tested ($p < 0.05$). Light levels beyond 30 μmol photons m^{-2} s^{-1} caused the growth rate to rapidly decrease again, becoming negative (cell death) between 100 and 120 μmol photons m^{-2} s^{-1} (Fig. 2).

Thermal curves

Interactive effects between light and thermal niche for this *Chaetoceros* isolate from the thermal performance curves at three different irradiance levels (15, 30, and 50 μmol photons m^{-2} s^{-1}) are shown in Fig. 3a and Table 1. Using a repeat measures

Table 1. Thermal performance curve parameters calculated at three light intensities. The units for width, minimum temperature for growth (T_{min}), maximum temperature for growth (T_{max}), and temperature with the fastest growth rate (T_{opt}) are °C while μ_{Max} shows specific growth rates (d^{-1}). SDs are shown where available, within parenthesis.

μmol photons m^{-2} s^{-1}	Width	T_{min}	T_{max}	T_{opt}	μ_{Max}	r^2
15	25.7	−2.0	23.7	13.7 (±0.87)	0.16 (±0.01)	0.87
30	27.0	−2.0	25.0	17.2 (±0.86)	0.28 (±0.02)	0.75
50	23.2	1.5	24.7	15.2 (±1.17)	0.25 (±0.02)	0.71

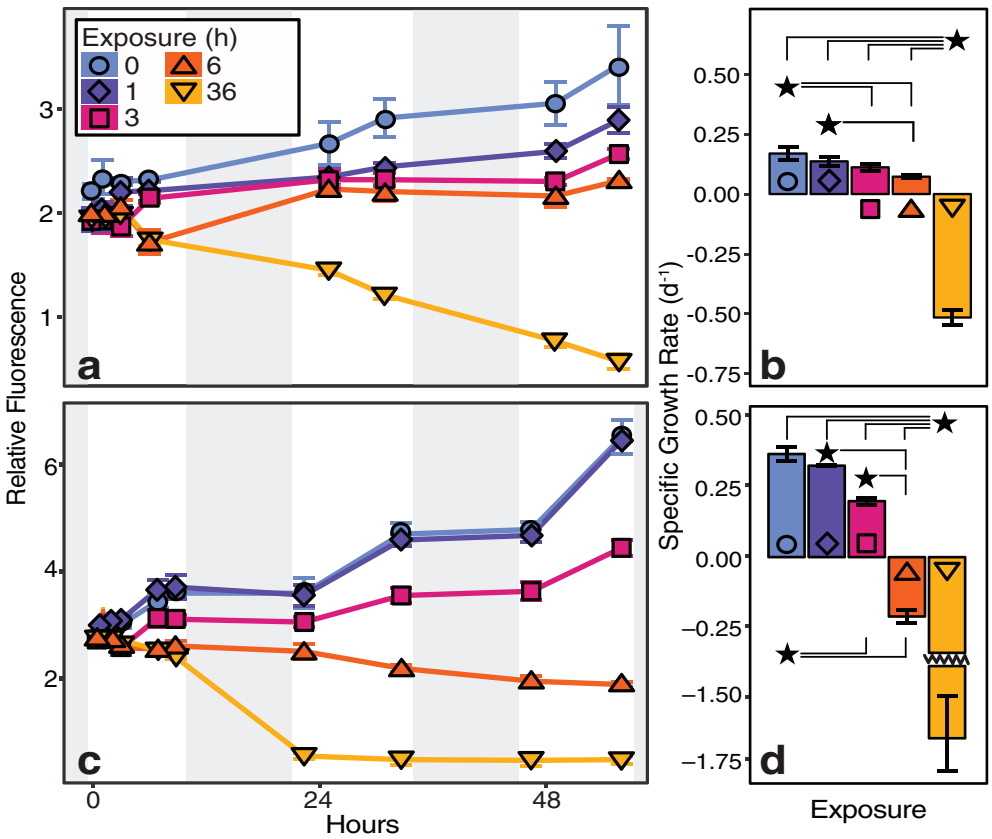

Fig 4. Effects of temperature and light exposure time on cultures of the novel Chaetoceros sp. isolate exposed to 638 µmol photons m^{-2} sec^{-1}, the highest incident light level recorded in 41 years of data from its isolation location. **a)** Fluorescence (RCF) and **b)** specific growth rates (day^{-1}) of cultures grown at 4°C under extreme light exposure. **c)** and **d)** show the same parameters for cultures grown under extreme light at 16°C. In panels a & c, periods of darkness are shown as grey bands. b & d depict the growth rates for each exposure treatment after three days. All error bars indicate ±1 standard deviation. Stars and brackets show treatments that are significantly different by one-way ANOVA and posthoc testing with Tukey's test ($p \leq 0.05$).

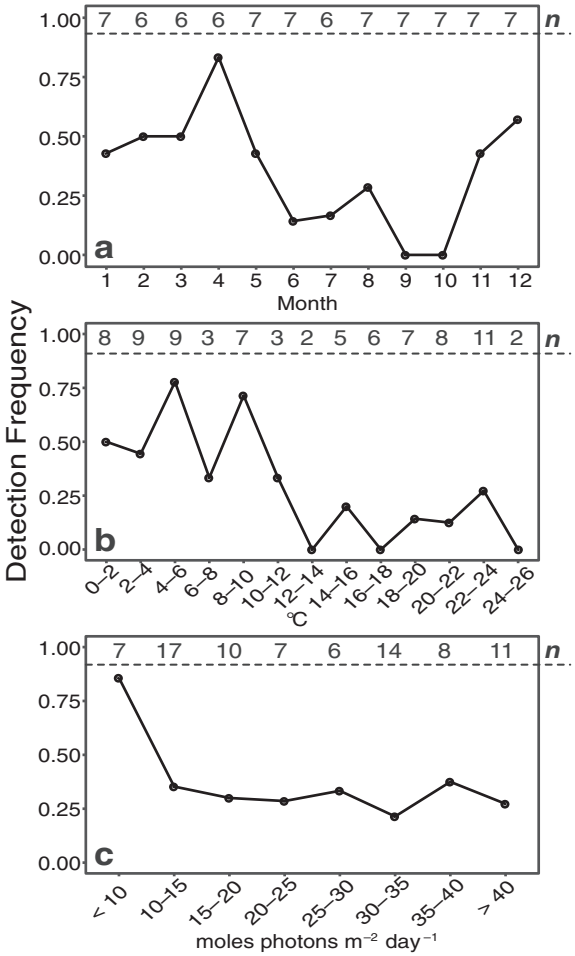

Fig 5. Detection frequency for the amplicon sequence variant (ASV) matching the isolate described in this study in six years of 18S rRNA gene amplicon data by **a)** month, **b)** temperature, and **c)** seven-day average of photons received per square meter. The number of samples falling within each category is shown along the top of each graph.

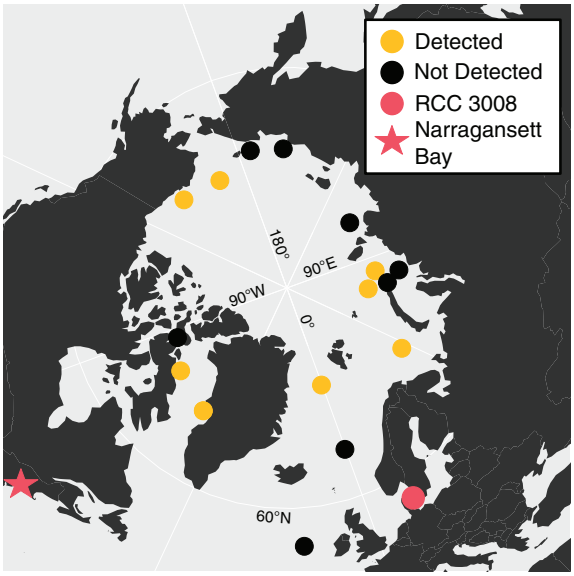

Fig 6. Combined relative abundance of two ASVs in the Tara Polar Ocean Circle stations that were a 100% match to the V9 region of the 18S rRNA gene sequence recovered from the diatom isolate presented in this study. The red circle shows the isolation location of a diatom in the Roscoff Culture Collection whose 18S rRNA gene is a close match to this isolate from Narragansett Bay (star).

ANOVA, each of these thermal performance curves was significantly different from each other (Fig. 3a, $p < 0.001$). Growth temperatures (the thermal niche width) was broadest at 15 and 30 μmol photons m^{-2} s^{-1} (27.0°C and 25.7°C, respectively), while at 50 μmol photons m^{-2} s^{-1} niche width was only 23.2°C (Table 1). The difference in modeled niche width compared to 30 μmol photons m^{-2} s^{-1} was manifested as a 1.3°C decrease in the highest temperature able to support growth (T_{max}) under low light (23.7°C), and as a 3.5°C increase in the lowest temperature able to support growth (T_{min}), under high light (1.5°C) (Table 1). The model predicted that the temperature with the fastest growth rate (T_{opt}) would be higher at 30 μmol photons m^{-2} s^{-1} (17.2°C ± 0.86; Fig. 3b, Table 1) than 15 and 50 μmol photons m^{-2} s^{-1} . Although it fell farther in low light, both 15 and 50 μmol photons m^{-2} s^{-1} light T_{opt} were within one standard deviation (SD) of each other (13.7 ± 0.87°C and 15.2 ± 1.17°C, respectively). The maximum specific growth rate (μ_{Max}) across these thermal performance curve models was estimated to be highest under 30 μmol photons m^{-2} s^{-1} and 50 μmol photons m^{-2} s^{-1} (0.28 d^{-1} ± 0.02 and 0.25 d^{-1} ± 0.02, respectively; Fig. 3c, Table 1).

Response to extreme light stress

In addition to considering how this diatom responded when acclimated to constant light and temperature conditions, we also assessed how it responded to pulses of extreme light at 4°C and 16°C. At both temperatures, constant exposure to extreme light levels (638 μmol photons m^{-2} s^{-1}) was lethal. At 4°C, the constant extreme light treatment (positive control) fluorescence decreased steadily until it reached the lower limit of detection at the very end of this experiment (Fig. 4a); however, at 16°C, fluorescence reached the lower limit after just 24 h (Fig. 4c), 3.3× faster (Fig. 4b,d). At the lower temperature this *Chaetoceros* isolate maintained positive growth even after being exposed to extreme light for 6 h, although exposure for both 3 and 6 h significantly decreased the growth rate compared to cultures never exposed to extreme light (negative control, $p < 0.05$). Similarly, measured growth rates were significantly lower after 3- and 6-h exposures compared with the negative control. Cells acclimated to 16°C also had significantly lower growth rates compared to unexposed cultures ($p < 0.05$); however, unlike at the colder temperature, exposure to extreme light for 6 h was lethal.

Environmental amplicon data

Before using the assembled 18S rRNA sequence to look for this diatom in available amplicon sequencing data from Narragansett Bay, we first confirmed that there was enough diversity within the V4 hypervariable region across this genus to distinguish our isolate from other *Chaetoceros* spp. Using aligned V4 regions of the same sequences in Fig. 1, we were able to construct a phylogenetic tree (Supporting Information Fig. S1) that separated our isolate from other members of the genus. Processing sequencing data from Narragansett Bay resulted in 5170 distinct ASVs; however, only 20 of these had an average relative abundance greater than 1% of recovered amplicons across the data set. When BLASTed, the most common diatom genera were *Thalassiosira* (eight), *Skeletonema* (four), and *Minidiscus* (two) (Supporting Information Table S2). These are consistent with previous observations at Narragansett Bay, where *Thalassiosira* and *Skeletonema* often dominate the diatom community (Canesi and Rynearson 2016; Rynearson et al. 2020). Of these 20 most abundant recovered ASVs, one was a perfect match (100% ID and 100% coverage) to the 18S rRNA gene sequence of our isolate.

This ASV was greater than 1% of the total recovered amplicons in 28 of the 80 samples. It had ca. 0.5 probability of detection in samples in January, February, and March (Fig. 5a). This probability peaked at 0.83 in April, before decreasing to 0.43 again in May. In June through August, the probability of detection was ca. 0.2 and dropped to zero in September and October, before rising again to 0.5 in November and December (Fig. 5a). Across all 80 samples, it comprised on average 4.1% of the relative diatom sequence reads per sample, with a maximum of 76.8% of recovered amplicons on May 28th, 2010 (Supporting Information Fig. S2). From the available observational data, we were not able to associate this isolate with major phytoplankton blooms in Narragansett Bay. In this data set, Chl *a* concentrations were greater than 10 μg L^{-1} in 10 different samples. The ASV matching our *Chaetoceros* isolate was only detected above the 1% relative abundance in three of these high Chl *a* events, but in each of these samples where it was detected it never made up more than 1.5% of the recovered amplicons.

To examine the thermal and light niches of the ASV matching our *Chaetoceros* isolate, we split temperatures into 13 two-degree bins from 0°C to 26°C. The isolate was present in Narraganset Bay from 0 C to 24 C but occurred more frequently at temperatures < 12°C. At these cooler temperatures, the probability of observing this ASV was on average 0.52 (± 0.19), but dropped to 0.11 (± 0.11) above 12°C, almost five times lower. The distribution of light exposure readings throughout the data set was largely 10–40 mol photons m^{-2} d^{-1}, so measurements within this range were grouped in increments of 5 mol photons m^{-2} d^{-1}, with readings outside this distribution recorded as < 10 mol photons m^{-2} d^{-1} and > 40 mol photons m^{-2} d^{-1}, respectively. The probability of detection was approximately equal at ca. 0.3 for all total irradiance levels > 10 mol photons m^{-2} d^{-1}; however, when total irradiance was < 10 mol photons m^{-2} d^{-1}, the probability of detection nearly tripled to 0.9 (Fig. 5c).

In order to assess this isolate's geographic distribution beyond Narragansett Bay, we accessed amplicon data from the Tara Oceans data set. Prior to analysis, a phylogenetic tree was made using the V9 region of the 18S rRNA genes used in Fig. 4 to show that these primers were able to differentiate our isolate from other *Chaetoceros* spp. (Supporting Information Fig. S3). This isolate was not detected in previously published amplicon data from the Tara Oceans project, which largely cover tropical and temperate latitudes (Callahan et al. 2017). However, two ASVs that were 100% match across > 90% of the sequence were detected in surface waters at 8 of 16 stations of the high-latitude Tara Oceans Polar Circle sampling (Fig. 6). Both ASVs were found at the same stations with approximately equal relative abundance, and thus their results are reported together. Interestingly, they were mostly detected at stations where the relative abundance of diatom amplicons was comparatively low (Supporting Information Fig. S4).

Discussion

In this study, we describe a recently isolated nano-diatom with 18S rRNA gene sequence similarity to diatoms identified as *Chaetoceros cf. wighamii* in NCBI. In laboratory culture experiments, this isolate showed a strong sensitivity to even moderate levels of light, which is unusual for planktonic diatoms. Indeed light levels greater than 100 μmol photons m^{-2} s^{-1} being lethal is even unusual among reports of other *Chaetoceros* species isolated from the Arctic Ocean, which have routinely used significantly higher light levels (Lacour et al. 2019; Lomas et al. 2019; Schiffrine et al. 2020). Light sensitivity also impacted the sensitivity of this *Chaetoceros* sp. to temperature changes, and conversely temperature also appeared to modulate its sensitivity to light stress. This interaction likely explains this diatom's seasonal distribution across multiple years of 18S rRNA gene amplicon data from its isolation location. Despite this seemingly unusual physiology, this *Chaetoceros* sp. was detected across the samples taken during the Tara Oceans Polar Circle Expedition. This suggests its physiology may not in fact be that unusual, but rather part of a broader adaption to high latitude waters.

A preference for low light levels for growth is not necessarily uncommon in marine phytoplankton. For instance, *Prochlorococcus*, a dominant unicellular marine picocyanobacterium in the oligotrophic gyres, has well-defined low- and high-light ecotypes occupying deep and surface layers of the euphotic zone, respectively (Moore et al. 1998; Goericke et al. 2000; Johnson et al. 2006). Studies on low light *Prochlorococcus* have reported upper light limits that are similar to those we describe here for our diatom isolate (Goericke et al. 2000). Even among diatoms, adaptations to low light levels have been reported in species living in benthic environments (Admiraal 1976). However, centric

diatoms are not typically considered to be part of the benthic community (although dormant resting stages can be observed) (Conley et al. 1989; Ligowski 2000; McQuoid and Godhe 2004). Alternately, it could be that the low-light physiology of our *Chaetoceros* isolate is an adaptation to deeper layers of the photic zone, similar to low-light *Prochlorococcus*, but its consistent presence even in open ocean surface water samples from high latitudes does not support either conclusion. Another possibility is this diatom could be adapted to living under sea ice, where active photosynthesis can be maintained below 5 μmol photons m^{-2} s^{-1} (Seckbach 2007). However, this seems unlikely as temperate environments such as Narragansett Bay typically do not freeze over during the winter (Pineda et al. 2005).

We show that at sub- or supraoptimal light levels, the maximum thermally determined growth rate and the thermal optimum decrease. Similar observations have been made in a metanalysis of phytoplankton temperature-light effects, however at much higher light levels (Edwards et al. 2016). In temperate and high latitudes, temperature and light levels increase simultaneously as spring progresses into summer and day length and angle of solar incidence increase. Our data suggest that the realized niche of this diatom is defined by the negative interactive effect of both temperature and light. For instance, in 6 yr of amplicon data it was detected in ca. 45–80% of the samples taken between November and April, when temperatures are low and the days are relatively short. The frequency of detection in May could be explained by the fact that although day length is increasing, the waters in Narragansett Bay are still colder than summer and early fall conditions (mean = 15.5°C, SD = $\pm$ 2.7°C). In the summer months (June through September), it was only detected four times. That it was detected at all during these warmer, brighter months suggests that there may be additional environmental factors (such as nutrient availability) controlling its distribution. Interactions between light and temperature also explain why observations of this diatom in situ typically occur at temperatures well below the range of optimal growth temperatures predicted by our thermal performance curve models (13.7–17.2°C). It should be stated however that only five observations were made between 10°C and 14°C, and it could be that more samples in this range would change the frequency of detection.

It is interesting to consider how these experimental and seasonal data affect this diatom's distribution in the broader ocean. For instance, although this *Chaetoceros* sp. was detected in half of the Tara Oceans Polar Circle samples, these were collected between May and October. Based on the seasonality depicted in data from Narragansett Bay, this is when we would expect its abundance to be lowest. Consequently, they may be even more abundant in polar waters than observed here. Summertime surface-water temperatures across the Arctic Ocean is on average of 2.56°C in the Tara Oceans Polar Circle samples, which is typically cooler than average wintertime surface-water temperatures in Narragansett Bay (4.67°C). However, daily irradiance levels during the Arctic summer have been reported in ranges from 21 to 39 mol photons m^{-2} d^{-1} due to the near constant daylight (Pabi et al. 2008), compared to the ca. 5–25 mol photons m^{-2} d^{-1} we observed over 6 yr of data from Narragansett Bay. It should be noted that there may be differences in the light levels experienced by phytoplankton in the water column at these two sites, due to differences in the angle of solar incidence. In culture experiments, we observed that this diatom's growth rate decreased at similar temperatures when light was supraoptimal (Fig. 3a), which suggests that its physiology could be an adaptation to the cold and low-light conditions found during early spring months in the North Atlantic (Siegel et al. 2002; Boss and Behrenfeld 2010). Future studies using molecular methods to look at the composition of early spring blooms may show that this diatom contributes significantly to primary production at high latitudes.

Although this study documents this diatom's singular low-light niche, more work will be needed to investigate the mechanisms involved. For photosynthetic organisms, an accumulation of deleterious reactive oxygen species in the cell (in particular the chloroplast) is often seen following exposure to extreme irradiance (Wilhelm et al. 2014; Mizrachi et al. 2019). Under low light conditions, many diatoms photo-acclimate by increasing the size of their chloroplasts and the number of photosystems and antenna pigments they contain, in order to increase photon capture (Rosen and Lowe 1984; Lepetit et al. 2012; Strzepek et al. 2019). It could be that our low-light *Chaetoceros* has a limited ability to adjust its photosynthetic energy acquisition systems when exposed to high light, causing a harmful buildup of reactive oxygen species. Similarly, variation in the xanthophyll cycle (Ruban et al. 2004; Cartaxana et al. 2013) and production of reactive oxygen species-scavenging antioxidants (Cartaxana et al. 2013) could contribute to this planktonic diatom's unusual physiology. Reactive oxygen species damage to the cell has also been suggested to increase at higher temperatures, and thus could explain the increased susceptibility to acute light stress at higher temperatures (Larkindale and Knight 2002).

Future work should also consider the effect of light spectral quality on the irradiance and temperature interactions described here. In aquatic environments, not only is the total irradiance variable, but also the availability of specific wavelengths. Shorter wavelength blue light is less absorbed by water molecules, and thus penetrates farther into the water column than longer red wavelengths. Phytoplankton associated with low light environments such as deep water or beneath sea ice are often specialized for utilizing these higher energy wavelengths (Gosselin et al. 1990; Shimada et al. 1996). At higher latitudes and during the winter, solar elevation is lower compared to low latitudes or during the summer. This results in a lower angle of incidence, which causes more light to be reflected from the ocean's surface. However, this process is skewed toward longer wavelengths, which are preferentially reflected (Campbell and Aarup 1989). The implication is that phytoplankton at higher latitudes or during the winter season experience more blue light relative to red light. It would be interesting to test

whether these diatoms experience the same light sensitivity when grown under blue light as white light (as in this study).

The interactive effects of light and temperature on this diatom's growth in the lab and pattern of abundance in situ raise interesting questions about how marine phytoplankton will respond to rising temperatures associated with climate change. It is broadly suggested that organisms at high latitudes exist at temperatures well below their thermal optima, and therefore rising temperatures will be advantageous, increasing their growth rate (Thomas et al. 2012; Boyd et al. 2013). The average temperature at Narragansett Bay in the 6 yr of temperature data accompanying this amplicon data set is 12.4°C, below the optimal temperatures predicted by our three thermal performance curve models. However, because of the strong regulation of thermal niche by light level in this *Chaetoceros* sp., it could be that this isolate will not fare better with rising temperatures, as warmer conditions increase its susceptibility to light stress. In a shallow (8 m), well-mixed estuary such as Narragansett Bay this interaction between light and temperature may in fact shrink the range of months where growth of this diatom is feasible. For instance, it is frequently (appearing in > 40% of the samples) observed as late in the year as April and May, where day length is longer and solar elevation higher than during the winter months. Rising temperatures during those months may be harmful, increasing the diatom's susceptibility to light stress; although it may also be that rising temperatures will be advantageous during winter months (e.g., December to March) when light levels are seasonally low.

In the open ocean, this diatom's sensitivity to light may disadvantage it in a warmer future. Current models predict a shoaling of the thermocline at high latitudes, increasing light exposure by trapping phytoplankton closer to the surface (Riebesell et al. 2009). This is expected to increase overall photosynthetic growth, as high latitude phytoplankton are often considered light limited (Yun et al. 2012). However, the *Chaetoceros* isolate described here, which was observed across the polar circle challenges this paradigm. Future work at high latitudes should further investigate the abundance of this diatom (especially during early spring bloom conditions) in order to better predict how climate change will impact phytoplankton communities in these regions.

Our study highlights one facet of the largely unrecognized but almost limitless diversity that exists in marine phytoplankton communities. It is fascinating that a planktonic diatom with such a specialized light and temperature niche was discovered at the longest running phytoplankton time series in existence, highlights the relatively unexplored diversity of smaller plankton groups. This work also shows that light and temperature can interact to define a thermal niche. Even in species that thrive at comparatively high light levels, changes in light could similarly impact their response to changes in temperature and influence how they will fare in a warming ocean. Future studies should consider high light as an interactive variable along with other costressors, such as elevated temperatures and CO_2, when predicting how phytoplankton will respond to global change.

References

Abad, D., A. Albaina, M. Aguirre, A. Laza-Martínez, I. Uriarte, A. Iriarte, F. Villate, and A. Estonba. 2016. Is metabarcoding suitable for estuarine plankton monitoring? A comparative study with microscopy. Mar. Biol. **163**: 149. doi:10.1007/s00227-016-2920-0

Admiraal, W. 1976. Influence of light and temperature on the growth rate of estuarine benthic diatoms in culture. Mar. Biol. **39**: 1–9. doi:10.1007/BF00395586

Bankevich, A., and others. 2012. SPAdes: A new genome assembly algorithm and its applications to single-cell sequencing. J. Comput. Biol. **19**: 455–477. doi:10.1089/cmb.2012.0021

Berges, J. A., D. E. Varela, and P. J. Harrison. 2002. Effects of temperature on growth rate, cell composition and nitrogen metabolism in the marine diatom *Thalassiosira pseudonana* (Bacillariophyceae). Mar. Ecol. Prog. Ser. **225**: 139–146. doi:10.3354/meps225139

Bolger, A. M., M. Lohse, and B. Usadel. 2014. Trimmomatic: A flexible trimmer for Illumina sequence data. Bioinformatics **30**: 2114–2120. doi:10.1093/bioinformatics/btu170

Boss, E., and M. Behrenfeld. 2010. In situ evaluation of the initiation of the North Atlantic phytoplankton bloom. Geophys. Res. Lett. **37**: 1–5. doi:10.1029/2010GL044174

Boyd, P. W., and others. 2013. Marine phytoplankton temperature versus growth responses from polar to tropical waters–outcome of a scientific community-wide study. PLoS One **8**: e63091. doi:10.1371/journal.pone.0063091

Callahan, B. J., P. J. McMurdie, M. J. Rosen, A. W. Han, A. J. A. Johnson, and S. P. Holmes. 2016. DADA2: High-resolution sample inference from Illumina amplicon data. Nat. Methods **13**: 581–583. doi:10.1038/nmeth.3869

Callahan, B. J., P. J. McMurdie, and S. P. Holmes. 2017. Exact sequence variants should replace operational taxonomic units in marker-gene data analysis. ISME J. **11**: 2639–2643. doi:10.1038/ismej.2017.119

Campbell, J. W., and T. Aarup. 1989. Photosynthetically available radiation at high latitudes. Limnol. Oceanogr. **34**: 1490–1499. doi:10.4319/lo.1989.34.8.1490

Canesi, K. L., and T. A. Rynearson. 2016. Temporal variation of *Skeletonema* community composition from a long-term time series in Narragansett Bay identified using high-throughput DNA sequencing. Mar. Ecol. Prog. Ser. **556**: 1–16. doi:10.3354/meps11843

Capella-Gutiérrez, S., J. M. Silla-Martínez, and T. Gabaldón. 2009. trimAl: A tool for automated alignment trimming in large-scale phylogenetic analyses. Bioinformatics **25**: 1972–1973. doi:10.1093/bioinformatics/btp348

Cartaxana, P., N. Domingues, S. Cruz, B. Jesus, M. Laviale, J. Serôdio, and J. M. Da Silva. 2013. Photoinhibition in benthic diatom assemblages under light stress. Aquat. Microb. Ecol. **70**: 87–92. doi:10.3354/ame01648

Conley, D. J., S. S. Kilham, and E. Theriot. 1989. Differences in silica content between marine and freshwater diatoms. Limnol. Oceanogr. **34**: 205–212. doi:10.4319/lo.1989.34.1.0205

de Vargas, C., and others. 2015. Eukaryotic plankton diversity in the sunlit ocean. Science **348**: 1261605. doi:10.1126/science.1261605

Dong, H.-P., Y.-L. Dong, L. Cui, S. Balamurugan, J. Gao, S.-H. Lu, and T. Jiang. 2016. High light stress triggers distinct proteomic responses in the marine diatom *Thalassiosira pseudonana*. BMC Genomics **17**: 994. doi:10.1186/s12864-016-3335-5

Edgar, R. C. 2004. MUSCLE: Multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Res. **32**: 1792–1797. doi:10.1093/nar/gkh340

Edwards, K. F., M. K. Thomas, C. A. Klausmeier, and E. Litchman. 2016. Phytoplankton growth and the interaction of light and temperature: A synthesis at the species and community level. Limnol. Oceanogr. **61**: 1232–1244. doi:10.1002/lno.10282

Ewels, P., M. Magnusson, S. Lundin, and M. Käller. 2016. MultiQC: Summarize analysis results for multiple tools and samples in a single report. Bioinformatics **32**: 3047–3048. doi:10.1093/bioinformatics/btw354

Feng, Y., M. E. Warner, Y. Zhang, J. Sun, F.-X. Fu, J. M. Rose, and D. A. Hutchins. 2008. Interactive effects of increased pCO_2, temperature and irradiance on the marine coccolithophore *Emiliania huxleyi* (Prymnesiophyceae). Eur. J. Phycol. **43**: 87–98. doi:10.1080/09670260701664674

Field, C. B., M. J. Behrenfeld, J. T. Randerson, and P. Falkowski. 1998. Primary production of the biosphere: Integrating terrestrial and oceanic components. Science **281**: 237–240. doi:10.1126/science.281.5374.237

Fu, F.-X., E. Yu, N. S. Garcia, J. Gale, Y. Luo, E. A. Webb, and D. A. Hutchins. 2014. Differing responses of marine N_2 fixers to warming and consequences for future diazotroph community structure. Aquat. Microb. Ecol. **72**: 33–46. doi:10.3354/ame01683

Gilstad, M., and E. Sakshaug. 1990. Growth rates of ten diatom species from the Barents Sea at different irradiances and day lengths. Mar. Ecol. Prog. Ser. **64**: 169–173. doi:10.3354/meps064169

Goericke, R., R. J. Olson, and A. Shalapyonok. 2000. A novel niche for *Prochlorococcus* sp. in low-light suboxic environments in the Arabian Sea and the Eastern Tropical North Pacific. Deep-Sea Res. Part I Oceanogr. Res. Pap. **47**: 1183–1205. doi:10.1016/S0967-0637(99)00108-9

Gosselin, M., L. Legendre, J. Therriault, and S. Demers. 1990. Light and nutrient limitation of sea-ice microalgae (Hudson Bay, Canadian Arctic). J. Phycol. **26**: 220–232. doi:10.1111/j.0022-3646.1990.00220.x

Guillard, R. R. L. 1975. Culture of phytoplankton for feeding marine invertebrates, p. 29–60. *In* W. L. Smith and M. H. Chanley [eds.], Culture of marine invertebrate animals. Springer. Boston, MA. doi:10.1007/978-1-4615-8714-9_3

Hare, C. E., K. Leblanc, G. R. DiTullio, R. M. Kudela, Y. Zhang, P. A. Lee, S. Riseman, and D. A. Hutchins. 2007. Consequences of increased temperature and CO_2 for phytoplankton community structure in the Bering Sea. Mar. Ecol. Prog. Ser. **352**: 9–16. doi:https://doi.org/10.3354/meps07182

Hutchins, D. A., and F. Fu. 2017. Microorganisms and ocean global change. Nat. Microbiol. **2**: 17058. doi:10.1038/nmicrobiol.2017.58

Hutchins, D. A., J. K. Jansson, J. V. Remais, V. I. Rich, B. K. Singh, and P. Trivedi. 2019. Climate change microbiology—problems and perspectives. Nat. Rev. Microbiol. **17**: 391–396. doi:10.1038/s41579-019-0178-5

Jiang, H.-B., and others. 2018. Ocean warming alleviates iron limitation of marine nitrogen fixation. Nat. Clim. Change **8**: 709–712. doi:10.1038/s41558-018-0216-8

Johnson, Z. I., E. R. Zinser, A. Coe, N. P. McNulty, E. M. S. Woodward, and S. W. Chisholm. 2006. Niche partitioning among *Prochlorococcus* ecotypes along ocean-scale environmental gradients. Science **311**: 1737–1740. doi:10.1126/science.1118052

Kling, J. D., M. D. Lee, F. Fu, M. D. Phan, X. Wang, P. Qu, and D. A. Hutchins. 2019. Transient exposure to novel high temperatures reshapes coastal phytoplankton communities. ISME J. **14**: 413–424. doi:10.1038/s41396-019-0525-6

Lacour, T., P. I. Morin, T. Sciandra, N. Donaher, D. A. Campbell, J. Ferland, and M. Babin. 2019. Decoupling light harvesting, electron transport and carbon fixation during prolonged darkness supports rapid recovery upon re-illumination in the Arctic diatom *Chaetoceros neogracilis*. Polar Biol. **42**: 1787–1799. doi:10.1007/s00300-019-02507-2

Langmead, B., and S. L. Salzberg. 2012. Fast gapped-read alignment with Bowtie 2. Nat. Methods **9**: 357–359. doi:10.1038/nmeth.1923

Larkindale, J., and M. R. Knight. 2002. Protection against heat stress-induced oxidative damage in Arabidopsis involves calcium, abscisic acid, ethylene, and salicylic acid. Plant Physiol. **128**: 682–695. doi:10.1104/pp.010320

Leblanc, K., and others. 2018. Nanoplanktonic diatoms are globally overlooked but play a role in spring blooms and carbon export. Nat. Commun. **9**: 1–12. doi:10.1038/s41467-018-03376-9

Lepetit, B., R. Goss, T. Jakob, and C. Wilhelm. 2012. Molecular dynamics of the diatom thylakoid membrane under different light conditions. Photosynth. Res. **111**: 245–257. doi:10.1007/s11120-011-9633-5

Ligowski, R. 2000. Benthic feeding by krill, *Euphausia superba* Dana, in coastal waters off West Antarctica and in Admiralty Bay, South Shetland Islands. Polar Biol. **23**: 619–625. doi:10.1007/s003000000131

Lomas, M. W., S. E. Baer, S. Acton, and J. W. Krause. 2019. Pumped up by the cold: Elemental quotas and stoichiometry of cold-water diatoms. Front. Mar. Sci. **6**: 1–17. doi:10.3389/fmars.2019.00286

Lyle, M. 1988. Climatically forced organic carbon burial in equatorial Atlantic and Pacific Oceans. Nature **335**: 529–532. doi:10.1038/335529a0

McGinnis, S., and T. L. Madden. 2004. BLAST: At the core of a powerful and diverse set of sequence analysis tools. Nucleic Acids Res. **32**: W20–W25. doi:10.1093/nar/gkh435

McQuoid, M. R., and A. Godhe. 2004. Recruitment of coastal planktonic diatoms from benthic versus pelagic cells: Variations in bloom development and species composition. Limnol. Oceanogr. **49**: 1123–1133. doi:10.4319/lo.2004.49.4.1123

Mizrachi, A., S. Graff van Creveld, O. H. Shapiro, S. Rosenwasser, and A. Vardi. 2019. Light-dependent single-cell heterogeneity in the chloroplast redox state regulates cell fate in a marine diatom. Elife **8**: 1–27. doi:10.7554/eLife.47732

Moore, L. R., G. Rocap, and S. W. Chisholm. 1998. Physiology and molecular phylogeny of coexisting *Prochlorococcus* ecotypes. Nature **393**: 464–467. doi:10.1038/30965

Mulholland, M. R., and P. W. Bernhardt. 2005. The effect of growth rate, phosphorus concentration, and temperature on N_2 fixation, carbon fixation, and nitrogen release in continuous cultures of *Trichodesmium* IMS101. Limnol. Oceanogr. **50**: 839–849. doi:10.4319/lo.2005.50.3.0839

Norberg, J. 2004. Biodiversity and ecosystem functioning: A complex adaptive systems approach. Limnol. Oceanogr. **49**: 1269–1277. doi:10.4319/lo.2004.49.4_part_2.1269

Pabi, S., G. L. van Dijken, and K. R. Arrigo. 2008. Primary production in the Arctic Ocean, 1998-2006. J. Geophys. Res. Oceans **113**: 1998–2006. doi:10.1029/2007JC004578

Pachauri, R. K., and others. 2014. Climate Change 2014: Synthesis report. Contribution of working groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change. IPCC.

Pineda, J., C. DiBacco, and V. Starczak. 2005. Barnacle larvae in ice: Survival, reproduction, and time to postsettlement metamorphosis. Limnol. Oceanogr. **50**: 1520–1528. doi:10.4319/lo.2005.50.5.1520

Price, M. N., P. S. Dehal, and A. P. Arkin. 2009. FastTree: Computing large minimum evolution trees with profiles instead of a distance matrix. Mol. Biol. Evol. **26**: 1641–1650. doi:10.1093/molbev/msp077

R Core Team. 2019. R: A language environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. https://www.R-project.org

Riebesell, U., A. K. Rtzinger, and A. Oschlies. 2009. Sensitivities of marine carbon fluxes to ocean change. Proc. Natl. Acad. Sci. USA **106**: 20602–20609. doi:10.1073/pnas.0813291106

Rosen, B. H., and R. L. Lowe. 1984. Physiological and ultrastructural responses of *Cyclotella meneghiniana* (Bacillariophyta) to light intensity and nutrient limitation. J. Phycol. **20**: 173–183. doi:10.1111/j.0022-3646.1984.00173.x

Rstudio Team. 2020. RStudio: Integrated Development Environment for R. RStudio, PBC. Boston, MA.

Ruban, A., J. Lavaud, B. Rousseau, G. Guglielmi, P. Horton, and A. L. Etienne. 2004. The super-excess energy dissipation in diatom algae: Comparative analysis with higher plants. Photosynth. Res. **82**: 165–175. doi:10.1007/s11120-004-1456-1

Rynearson, T. A., S. A. Flickinger, and D. N. Fontaine. 2020. Metabarcoding reveals temporal patterns of community composition and realized thermal niches of *Thalassiosira* spp. (Bacillariophyceae) from the Narragansett Bay long-term plankton time series. Biology **9**: 1–19. doi:10.3390/biology9010019

Schiffrine, N., J. É. Tremblay, and M. Babin. 2020. Growth and elemental stoichiometry of the ecologically-relevant Arctic diatom *Chaetoceros gelidus*: A mix of polar and temperate. Front. Mar. Sci. **6**: 1–15. doi:10.3389/fmars.2019.00790

Seckbach, J. 2007. Algae and cyanobacteria in extreme environments. Astrobiology **786**: 343–364. doi:10.1007/978-1-4020-6112-7

Shimada, A., T. Maruyama, and S. Miyachi. 1996. Vertical distributions and photosynthetic action spectre of two oceanic picophytopianlcters, *Prochlorococcus marinus* and *Synechococcus* sp. Mar. Biol. **127**: 15–23. doi:10.1007/BF00993639

Siegel, D. A., S. C. Doney, and J. A. Yoder. 2002. The North Atlantic spring phytoplankton bloom and Sverdrup's critical depth hypothesis. Science **296**: 730–733. doi:10.1126/science.1069174

Smith, S. V., and J. T. Hollibaugh. 1993. Coastal metabolism and the oceanic organic carbon balance. Rev. Geophys. **31**: 75–89. doi:10.1029/92RG02584

Strzepek, R. F., P. W. Boyd, and W. G. Sunda. 2019. Photosynthetic adaptation to low iron, light, and temperature in Southern Ocean phytoplankton. Proc. Natl. Acad. Sci. USA **116**: 4388–4393. doi:10.1073/pnas.1810886116

Sunda, W. G., N. M. Price, and F. M. M. Morel. 2005. Trace metal ion buffers and their use in culture studies, p. 35–63. *In* R. A. Andersen [ed.], Algal culturing techniques. Academic Press. Cambridge, MA.

Thomas, M. K., C. T. Kremer, C. A. Klausmeier, and E. Litchman. 2012. A global pattern of thermal adaptation in marine phytoplankton. Science **338**: 1085–1088. doi:10.1126/science.1224836

Wilhelm, C., A. Jungandreas, T. Jakob, and R. Goss. 2014. Light acclimation in diatoms: From phenomenology to mechanisms. Mar. Genomics **16**: 5–15. doi:10.1016/j.margen.2013.12.003

Wood, A. M., R. C. Everroad, and L. M. Wingard. 2005. Measuring growth rates in microalgal cultures, pp. 269–288. *In* R. A. Andersen [ed.], Algal Culturing Techniques. Academic Press: Cambridge, MA.

Yun, M. S., K. H. Chung, S. Zimmermann, J. Zhao, H. M. Joo, and S. H. Lee. 2012. Phytoplankton productivity and its response to higher light levels in the Canada Basin. Polar Biol. **35**: 257–268. doi:10.1007/s00300-011-1070-6

Zhu, S.-H., and B. R. Green. 2010. Photoprotection in the diatom *Thalassiosira pseudonana*: Role of LI818-like proteins in response to high light stress. Biochim. Biophys. Acta **1797**: 1449–1457. doi:10.1016/j.bbabio.2010.04.003

Zimmermann, J., R. Jahn, and B. Gemeinholzer. 2011. Barcoding diatoms: Evaluation of the V4 subregion on the 18S rRNA gene, including new primers and protocols. Org. Divers. Evol. **11**: 173–192. doi:10.1007/s13127-011-0050-6

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Conflict of Interest

None declared.

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