Thermal Thresholds of Phytoplankton Growth in Polar Waters and Their Consequences for a Warming Polar Ocean

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Polar areas are experiencing the steepest warming rates on Earth, a trend expected to continue in the future. In these habitats, phytoplankton communities constitute the basis of the food web and their thermal tolerance may dictate how warming affects these delicate environments. Here, we compiled available data on thermal responses of phytoplankton growth in polar waters. We assembled 53 growth-vs.-temperature curves (25 from the Arctic, 28 from the Southern oceans), indicating the limited information available for these ecosystems. Half of the data from Arctic phytoplankton came from natural communities where low ambient concentrations could limit growth rates. Phytoplankton from polar waters grew faster under small temperature increases until reaching an optimum (T_{OPT}), and slowed when temperatures increased beyond this value. This left-skewed curves were characterized by higher activation energies (E_a) for phytoplankton growth above than below the T_{OPT}. Combining these thermal responses we obtained a community T_{OPT} of 6.5°C (±0.2) and 5.2°C (±0.1) for Arctic and Southern Ocean phytoplankton communities, respectively. These threshold temperatures were already exceeded at 70°N during the first half of August 2013, evidenced by sea surface temperatures (SSTs, satellite data, http://www.ncdc.noaa.gov). We forecasted SSTs for the end of the twenty-first century by assuming an overall 3°C increase, equivalent to a low emission scenario. Our forecasts show that SSTs at 70°N are expected to exceed T_{OPT} during summer by 2100, and during the first half of August at 75°N. While recent Arctic spring temperatures average 0.5°C and −0.7°C at 70°N and 75°N, respectively, they could increase to 2.8°C at 70°N and 2.2°C at 75°N as we approach 2100. Such temperature increases could lead to intense phytoplankton blooms, shortened by fast nutrient consumption. As SSTs increase, thermal thresholds for phytoplankton growth would be eventually exceeded during bloom development. This could lead to changes in the blooming phytoplankton community, threatening the production peak and cycles in the Arctic. Our forecasted phytoplankton responses, are constrained by the limited data set, besides uncertainties in the most plausible future Arctic temperature scenarios. To improve predictions in polar oceans, we need to increase the number of studies, in particular for a fast-changing Arctic.

Keywords: phytoplankton, polar oceans, thermal threshold, climate change, spring bloom

INTRODUCTION

Climate change is predicted to increase average global temperatures by 0.3–0.9°C per decade. Polar regions are expected to experience the highest temperature increases (Christensen et al., 2007), with far-reaching effects on the Arctic (Wassmann and Reigstad, 2011). Furthermore, an acceleration of temperature increases is also anticipated in some regions (around the Antarctic Peninsula and near-coastal Antarctica) of the Southern Ocean (Christensen et al., 2007).

The ecological and physiological adaptations of phytoplankton to temperature influence their global distribution (Huertas et al., 2011; Thomas et al., 2012). The effect of temperature on phytoplankton growth has been widely observed (Raven and Geider, 1988; Coello-Camba et al., 2014, 2015). The thermal performance curves of these organisms usually follow a typical shape of being bound at extreme temperatures with a single intermediate mode (Angilletta, 2006; **Figure 1**). This mode represents the optimum temperature (T_{OPT}) for growth. The farther away the temperature moves from this optimum, the lower the growth rate. Phytoplankton communities account for most primary production in the oceans (Sakshaug and Holm-Hansen, 1984). These pelagic organisms have optimum temperatures for growth that are strongly related to mean annual temperatures at their geographical location, demonstrating a clear latitudinal trend in their T_{OPT} (Thomas et al., 2012), with higher T_{OPT} for growth at lower and hence warmer latitudes. Warming is therefore expected to cause poleward shifts in the range of species (Parmesan, 2006; Thomas et al., 2012) as they vary their biogeographic distribution to accommodate changes in ambient temperatures (Loarie et al., 2009; Burrows et al., 2011). Nonetheless, for species inhabiting polar oceans no "colder waters" will be available as refugia (Boyd et al., 2013). The high-latitude niches occupied by species with low T_{OPT} values will diminish, necessitating that these species acclimatize or adapt to higher temperatures to survive (Boyd et al., 2013). Besides this, an increase in the number of subpolar phytoplankton species moving into the polar region is likely to happen, particularly in the Arctic Ocean, where advection processes help to connect this ocean with waters at lower latitudes (Hunt et al., 2016). Under such conditions, competition will become a strong selection factor as the environment becomes better suited to incoming species from lower latitudes and resident communities will be challenged.
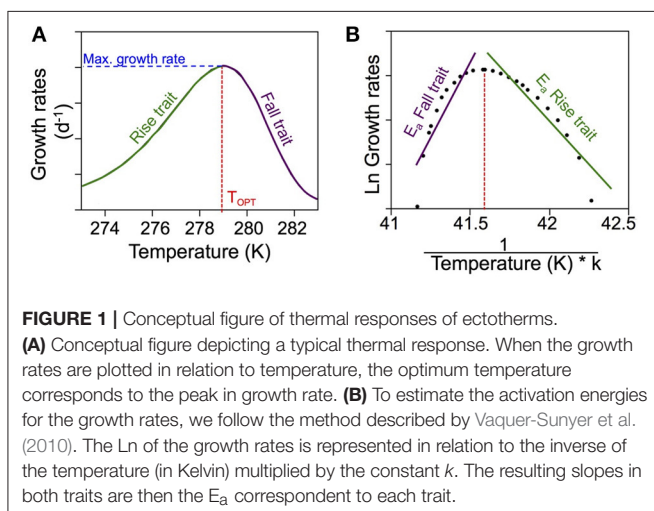
Although thermal performance curves have been described for several organisms (Loarie et al., 2009), few datasets presenting thermal curves for polar phytoplankton are available (i.e., Thomas et al., 2012). This may be a consequence of the remoteness of polar waters and of the limited number of polar phytoplankton species that have successfully been cultured in the laboratory.

The goal of this paper is to identify the thermal thresholds of phytoplankton in polar waters and to predict possible implications of increasing temperatures for growth and bloom development. To do so, we created a growth-vs.-temperature database using data from the literature and new experiments. Then, based on this database, we calculated the community T_{OPT} for growth, a parameter that represents a turning point beyond which temperature becomes a restrictive factor. We also calculated activation energies (E_a) to illustrate the steepness of the changes in growth rates above and below the optimum temperature and to infer the capacity for phytoplankton to respond to increased temperature in a warming polar sea. We then compared thermal thresholds with recent surface seawater temperatures (SSTs) in both polar oceans to evaluate how close phytoplankton populations are to their thermal limits. Finally, we modeled a future SST scenario to predict when temperatures will rise above the thermal thresholds of phytoplankton in polar waters. Temperature predictions will be especially relevant to the Arctic and to the spring bloom, a key process that accounts for the largest part of annual primary production (Leu et al., 2011) and that is tightly coupled with melting ice (Leu et al., 2011). Alterations in the timing and/or quality of this key peak in primary production may consequently alter Arctic food webs and possibly influence biogeochemical cycles.

MATERIALS AND METHODS

Seawater Temperature

Recent SSTs for the entire Arctic Ocean were obtained from satellite data (http://www.ncdc.noaa.gov). We averaged daily temperatures from four latitudes (70, 75, 80, and 85°N) between March and September 2013 to gain a general representation of Arctic SSTs. For the Southern Ocean, we considered the SSTs measured during the same year in the vicinity of the Antarctic Peninsula (80–50°W, 75°S-Antarctic Convergence). To estimate future SSTs in these areas, we increased the SSTs observed in 2013 by 3°C, taking into account that seawater temperatures will remain low as long as the ice cover remains and that they will gradually increase after the ice melts. This represents a low-emission scenario similar to that previously assumed by various authors (e.g., Flombaum et al., 2013). This 3°C increase corresponds to an intermediate value between the increase in temperatures predicted for the Arctic by the RCP2.6 (+2.2°C) and RCP4.5 (+4.2°C) scenarios estimated in the Fifth

FIGURE 1 | Conceptual figure of thermal responses of ectotherms. **(A)** Conceptual figure depicting a typical thermal response. When the growth rates are plotted in relation to temperature, the optimum temperature corresponds to the peak in growth rate. **(B)** To estimate the activation energies for the growth rates, we follow the method described by Vaquer-Sunyer et al. (2010). The Ln of the growth rates is represented in relation to the inverse of the temperature (in Kelvin) multiplied by the constant k. The resulting slopes in both traits are then the E_a correspondent to each trait.

Assessment Report of the Intergovernmental Panel on Climate Change (IPCC; Collins et al., 2013).

Dataset from the Literature

We assembled a dataset of marine phytoplankton growth rates vs. temperature to estimate the optimal growth temperatures (T_{OPT}) for phytoplankton in the Arctic and Southern Oceans. This dataset included bibliographic and new experimental data. During the literature search, we took into account all studies published to that date that reported growth rate measurements of polar marine phytoplankton at different temperatures. To determine which data should be included in our analyses, we used the following criteria: following the climatic classification proposed by Supan (1884), we considered phytoplankton species living beyond the 10°C isotherm defined for the warmest month as Arctic species. For Antarctic species, we selected those living beyond the Antarctic Convergence, an oceanographic barrier that delimits the Southern Ocean and varies between 50 and 65°S (Anisimov et al., 2001; **Figure 2**). We focused our analysis on those studies that evaluated temperature increases consistent with possible future scenarios in both polar areas and excluded measurements at high temperatures that would be unlikely to happen in these oceans within the next century. Due to the limited number of polar studies meeting the requirements needed for our study, we also considered those studies in which the largest measured growth rates occurred at the lowest or highest temperature tested. Also, we preferentially selected data obtained under experimental conditions (of light, salinity, etc.) that were more similar to the natural levels usually encountered in these oceans. The resulting dataset is detailed in **Table 1**.

Experimental Data

We performed four experiments on natural phytoplankton communities during the ATOS-I and ESASSI cruises on the Arctic and Southern Oceans, respectively, on board the Spanish research vessel *BIO Hespérides.* ATOS-I (Atmospheric inputs of organic carbon and pollutants to the polar ocean: rates, significance and outlook) took place between 29 June and 27 July 2007 across the Fram Strait, between the Spitsbergen Islands and the ice limit. The ESASSI [Spanish contribution to the SASSI ("Synoptic Antarctic Shelf-Slope Interaction") international project] cruise took place the following year, from 2 to 23 January 2008 in the South Scotia Ridge region.

During each cruise, surface seawater samples (5 m depth) were collected using 12-L Niskin bottles attached to a CTD-rosette system and distributed into six 2-L bottles, adding plankton collected from a 20-μm net. These samples were incubated at three different temperatures, with the lowest temperature treatment similar to the *in situ* seawater temperature measured at the beginning of the experiment and the other temperatures representing two steps of 2–3 and 4–5°C higher. Polycarbonate bottles were incubated in white 50-L tanks placed on deck of the ship to receive natural solar radiation. These bottles reduced photosynthetically active radiation (PAR) by 10%. They were secured with a light net that additionally removed 18% of PAR; this way, our incubations were exposed to light conditions close to the PAR levels found at 5 m depth. These tanks were filled with seawater and connected to a cooling circulating water system and a thermostat (Lauda Co.) to maintain the desired temperature (error ± 0.5°C). The precision of the system was regularly checked with a digital thermometer.

The nutrient concentrations measured in our experiments allowed the growth of phytoplankton during the incubations. Phytoplankton cell abundances were measured every second day. A known volume (20–50 mL) from each experiment was filtered through a black polycarbonate filter (1 μm pore) and fixed with glutaraldehyde (1% final concentration). Cells were counted at x1000 magnification using an Olympus BX40 and a Zeiss Axiovert 25 epifluorescence microscope. Cell abundances
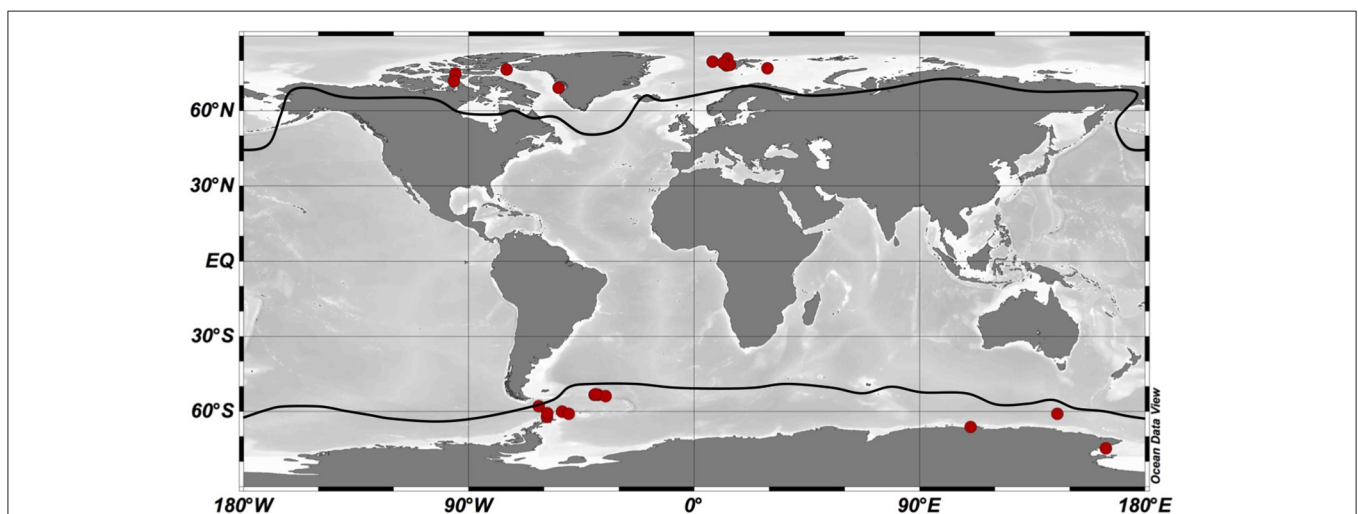

FIGURE 2 | Geographical distribution of optimum temperature data for phytoplankton growth in the Arctic and Southern Oceans. Red dots indicate geographical sites from which phytoplankton species where isolated. Dark lines represent the polar boundaries considered in this study: the 10°C isotherm for the Arctic Ocean and the Antarctic Convergence for the Southern Ocean. Schlitzer, R., Ocean Data View, http://odv.awi.de, 2015.

TABLE 1 | Optimum temperatures (T_{OPT}) and maximum growth rates (μ_{max}) estimated for Arctic and Antarctic phytoplankton.

Species/Group	Coordinates	Temperature interval (°C)	T_{OPT} (°C)	Maximum growth rates (d^{-1})	References	Temperature steps (°C)	
ARCTIC OCEAN							
Centric diatoms 7 μm	78°N/13°E	1.82 to 10.32	10.32	0.17	Coello-Camba et al., 2014	4–5	n
Centric diatoms 7 μm	76.79°N/29.33°E	1.6 to 10.45	4.47	0.14	Coello-Camba et al., 2015	1.5	n
Chaetoceros sp.	80.79°N/13.31°E	2 to 8	8	0.52	This study	3	n
Chaetoceros sp.	74.65°N/95.2°W	−1.8 to 15	5	0.57	Suzuki and Takahashi, 1995	4 (approx.)	c
Dinobryon sp.	80.79°N/13.31°E	2 to 8	8	0.43	This study	3	n
Flagellates 20 μm	76.79°N/29.33°E	1.6 to 10.45	10.45	0.17	Coello-Camba et al., 2015	1.5	n
Flagellates 20 to 50 μm	76.79°N/29.33°E	1.6 to 10.45	4.47	0.03	Coello-Camba et al., 2015	1.5	n
Flagellates 3 to 6 μm	76.79°N/29.33°E	1.6 to 10.45	5.55	0.15	Coello-Camba et al., 2015	1.5	n
Flagellates 3 to 6 μm	78.25°N/14.4°E	1.15 to 9.95	9.95	0.36	Coello-Camba et al., 2015	1.5	n
Fragillariopsis cylindrus (strain D3G1)	69.18°N/53.52°W	1 to 8	8	0.33	Pančić, 2015	3–4	c
Fragillariopsis cylindrus (strain D4D11)	69.18°N/53.52°W	1 to 8	8	0.58	Pančić, 2015	3–4	c
Fragillariopsis cylindrus (strain D10A12)	69.18°N/53.52°W	1 to 8	8	0.83	Pančić, 2015	3–4	c
Micromonas sp.	76.28°N/74.75°W	0 to 12	8	0.55	Lovejoy et al., 2007	2	c
Micromonas sp.	76.79°N/29.33°E	1.6 to 10.45	5.55	0.13	Coello-Camba et al., 2015	1.5	n
Micromonas sp.	78.25°N/14.4°E	1.15 to 9.95	3.02	0.25	Coello-Camba et al., 2015	1.5	n
Nitzschia frigida	74.65°N/95.2°W	−1.8 to 10	2	0.42	Suzuki and Takahashi, 1995	4 (approx.)	c
Phaeocystis pouchetii	≈81°N/10°E	1.5 to 12	12	0.55	Jahnke, 1989	2–6	c
Phaeocystis sp.	76.79°N/29.33°E	1.6 to 10.45	10.45	0.18	Coello-Camba et al., 2015	1.5	n
Phaeocystis sp.	79.52°N /7.44°W	4 to 8	4	0.13	This study	2	n
Pseudo-nitzschia seriata	71.68°N/95.83°W	−1.5 to 10	6	0.49	Stapleford and Smith, 1996	2–4 (approx.)	c
Pyramimonas sp.	78°N/13°E	1.82 to 10.32	1.8	0.41	Coello-Camba et al., 2014	4–5	n
Thalassiosira sp.	80.79°N/13.31°E	2 to 8	5	0.06	This study	3	n
Whole phytoplankton community	76.79°N/29.33°E	1.6 to 10.45	1.6	0.04	Coello-Camba et al., 2015	1.5	n
Whole phytoplankton community	78.25°N/14.4°E	1.15 to 9.95	5.48	0.31	Coello-Camba et al., 2015	1.5	n
Whole phytoplankton community	80.79°N/13.31°E	2 to 8	5	0.4	This study	3	n
SOUTHERN OCEAN							
Chaetoceros sp.	40 to 66°S/66.30°W	3 to 10	7	0.5	Jacques, 1983	2–3	c
Chlamydomonas sp.	66.28°S/110.48°E	4 to 30	9	0.4	Teoh et al., 2004	2–5–10 (approx.)	c
Corethron pennatum*	58°S/62°W	0 to 6	4	0.25	Fiala and Oriol, 1990	2	c
Fragilariopsis cylindrus	58°S/62°W	0 to 9	5	0.57	Fiala and Oriol, 1990	1–3	c
Fragilariopsis kerguelensis	58°S/62°W	0 to 7	4	0.52	Fiala and Oriol, 1990	2	c
Fragilariopsis kerguelensis	40 to 66°S/66.30°W	3 to 7	5	0.34	Jacques, 1983	2	c
Gyrosigma subsalinum	62.23°S/58.63°W	0 to 10	0	0.27	Longhi et al., 2003	1–5	c
Klebsormidium sp.	66.28°S/110.48°E	4 to 30	14	0.25	Teoh et al., 2004	2–5–10 (approx.)	c
Koliella antarctica	74.8°S/164.5°E	0 to 20	12.5	0.3	Vona et al., 2004	5	c
Nanoflagellates pop. 1	60.94°S/50.03°W	1 to 6	6	0.36	This study	2–3	n
Nanoflagellates pop. 2	60.94°S/50.03°W	1 to 6	6	0.36	This study	2–3	n
Navicula sp.	66.28°S/110.48°E	4 to 30	4	0.34	Teoh et al., 2004	2–5–10 (approx.)	c

(Continued)

TABLE 1 | Continued

Species/Group	Coordinates	Temperature interval (°C)	T$_{OPT}$ (°C)	Maximum growth rates (d^{-1})	References	Temperature steps (°C)	
Odontella litigiosa	62.23°S/58.63°W	0 to 10	0	0.42	Longhi et al., 2003	1–5	c
Phaeocystis sp.	(Weddell Sea)	2 to 7	2	0.79	Buma et al., 1991	5	c
Proboscia inermis	61°S/145°E	1 to 10	5	0.33	Boyd et al., 2013	1	c
Pseudo-nitzschia turgiduloides	58°S/62°W	1 to 8	3	0.5	Fiala and Oriol, 1990	1–2	c
Pseudo-nitzschia turgiduloides**	40 to 66°S/66.30°W	3 to 7	5	0.32	Jacques, 1983	2	c
Stellarima microtrias	58°S/62°W	1 to 7	4	0.56	Fiala and Oriol, 1990	3	c
Synedra sp.	58°S/62°W	1 to 7	5	0.38	Fiala and Oriol, 1990	2–4	c
Thalassiosira sp.	60.16°S/52.67°W	1 to 6	6	0.6	This study	3–4	n
Thalassiosira sp.	60.94°S/50.03°W	1 to 6	4	0.45	This study	3–4	n
Whole phytoplankton community	53.96°S.35.32°W	2 to 8	8	2.61	Reay et al., 2001	3	n
Whole phytoplankton community	53.4°S.38.23°W	3 to 9	9	0.69	Reay et al., 2001	3	n
Whole phytoplankton community	53.18°S.39.23°W	2.5 to 8.5	5.5	0.64	Reay et al., 2001	3	n
Whole phytoplankton community	53.47°S.39.66°W	3.5 to 9.5	6.5	0.35	Reay et al., 2001	3	n
Whole phytoplankton community	60.16°S.52.67°W	1 to 6	6	0.27	This study	2–3	n
Whole phytoplankton community	60.94°S.50.03°W	1 to 6	4	0.4	This study	2–3	n
Whole phytoplankton community	60.78°S.58.60°W	−2 to 8	5	0.82	Tilzer and Dubinsky, 1987	2–3	n

*, ** these species were named as Corethron criophilum and Nitzschia turgiduloides in the original publication; Fiala and Oriol (1990). The temperature steps between treatments are also indicated. Data obtained from natural communities are marked with (n) and those obtained from phytoplankton grown in laboratory cultures are marked with (c). Growth data from natural Arctic communities are conditioned by low natural nutrient concentrations.

for the smallest phytoplankton groups in the Southern Ocean samples were counted using a FACSCalibur (Becton Dickinson) flow cytometer equipped with a 488-nm laser. To count the largest cells we used a FlowCAM (FluidImaging Technologies), equipped with a 300-μm-wide flow cell and a camera with a 4x magnification objective. We estimated the abundance of the particles by relating the cell counts to the volume of sample processed.

To estimate the biomass of the whole phytoplankton community, we measured chlorophyll *a* concentrations. We filtered 50 mL of experimental water into Whatman GF/F filters daily and followed the fluorometric method described by Parsons et al. (1984).

Growth vs. Temperature Curves and Identification of T$_{OPT}$

We estimated the T$_{OPT}$ for growth in polar phytoplankton communities from the optimum temperatures of the different groups and communities described in our database. We took into account the fact that T$_{OPT}$ values for growth are robust across a range of different experimental methodologies (Boyd et al., 2013).

To estimate T$_{OPT}$ during our experiments, we calculated the net growth rates (μ) for each group and for the whole

phytoplankton community under every temperature treatment. These were calculated from the slope of changes in the natural logarithm (Ln) of the cell abundance (N) (or of their chlorophyll *a* concentration, chl *a*), over the duration of the experiment (days, t) by fitting the following linear regression equation:

$$Ln\,(N_t) = a + \mu t \qquad (1)$$

Then, we obtained each specific T$_{OPT}$ from the growth rates obtained from our experiments and from the previous studies included in our polar database that did not directly include the optimum temperature. We chose the tested temperature at which the maximum net growth rate occurred (gross growth rates for those studies using cultures; **Figure 1A**).

To calculate the T$_{OPT}$ of Arctic and Southern Ocean communities, we plotted each T$_{OPT}$ from the database against its correspondent maximum growth rate and fit three functions to the upper limit of the scattering data. We applied the unimodal function described by Johnson and Lewin in 1946 (Dell et al., 2011; Equation 2) and the Gaussian and Weibull functions (Angilletta, 2006; Equations 3, 4). We used JMP® statistics software and followed an iterative mathematical method, the Gauss-Newton algorithm, with a stop limit of 2,000 iterations. This method requires a series of initial

values for each parameter to work. Here, we arbitrarily assigned these values such that they were low enough to allow the algorithm to perform properly and cover all the data range, which improved convergence and parameter estimation.

Each function provided an overall T_{OPT} value, which we averaged to obtain a mean optimum temperature for both Arctic and Southern Ocean communities as a whole.

$$h(T) = \frac{ce^{-\frac{E}{kT}}}{1 + e^{-\frac{1}{kT}\left(E_D - \left(\frac{E_D}{T_{OPT}} + k\, ln\left(\frac{E}{E_D - E}\right)\right)T\right)}} \quad (2)$$

$$h(T) = ae^{\left[-0.5\left(\frac{|T - b|}{c}\right)^2\right]} \quad (3)$$

$$h(T) = a\left(\frac{d-1}{d}\right)^{\frac{1-d}{d}}\left[\frac{T-b}{c} + \left(\frac{d-1}{d}\right)^{\frac{1}{d}}\right]^{d-1}$$

$$e^{-\left[\left(\frac{T-b}{c}\right) + \left(\frac{d-1}{d}\right)^{\frac{1}{d}}\right]^d} + \frac{d-1}{d} \quad (4)$$

Activation Energies

The activation energies (E_a) were calculated for the growth-vs.-temperature curves obtained for each group and community. To estimate the activation energies for the rise and fall traits, we divided the growth-vs.-temperature curves into two parts, one below the optimum temperature (rise trait) and the other above this value (fall trait). E_a values (in eV) were then estimated from the slope of the Arrhenius equation relating the natural logarithm of growth rates (in d^{-1}) to the inverse of the growth temperature (in Kelvin) multiplied by k (Boltzmann's constant, $8.62 \cdot 10^{-5}$ eV k^{-1}) as described by Vaquer-Sunyer et al. (2010) (**Figure 1B**). The resulting E_a values were grouped separately for Arctic and Southern Ocean data.

RESULTS

Temperature Optima

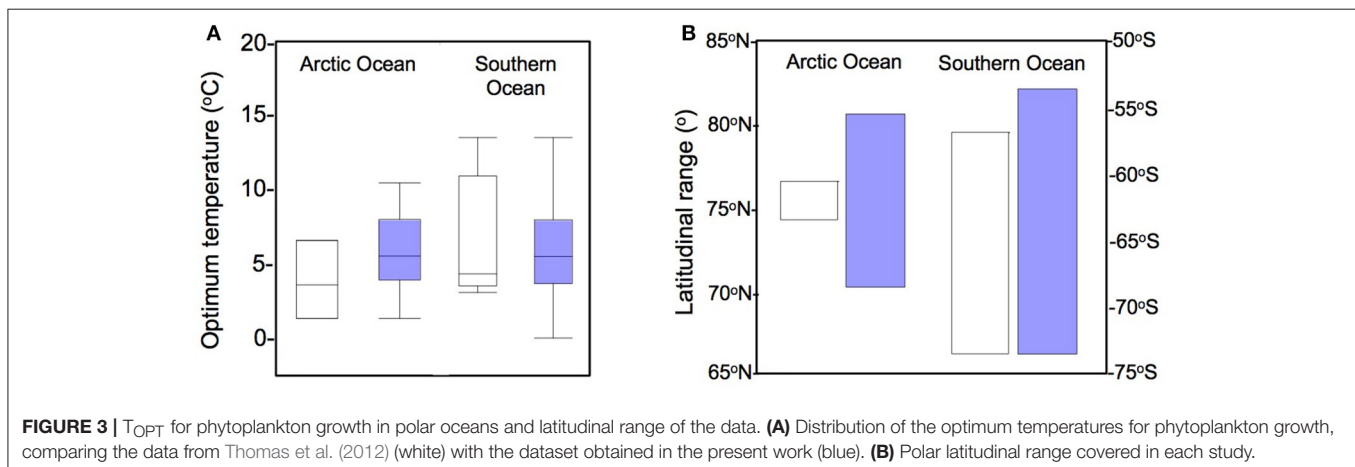We compiled 53 estimations of the relationship between the growth rates of phytoplankton from polar waters and increasing temperature: 11 from our own experiments and 42 from the literature (16 papers published between 1983 and 2015). From that total, 25 measurements corresponded to Arctic communities and 28 corresponded to the Southern Ocean communities (**Figure 2**). In both phytoplankton communities from the Arctic and Southern Oceans, there were diatoms such as *Thalassiosira* spp., *Chaetoceros* spp., and *Fragilariopsis cylindrus. Phaeocystis* spp. and *Micromonas* spp. stood out among the flagellate cells as also being present in both polar communities.

When the studies considered here covered the whole thermal range of the phytoplankton group studied, the resulting thermal performance curves usually exhibited a characteristic shape, with higher growth rates at the intermediate temperatures tested. In some cases, the temperature interval was not wide enough, and the highest growth rates observed occurred at the extremes of the temperature range tested. This contributed to the lower amount of data available for estimating the E_a fall trait and generated errors in the detection of the T_{OPT} of that phytoplankton group.

Among the maximum net growth rates compiled here, we found low values for some of the groups studied in the Arctic ocean (e.g., flagellates 20–50 μm, **Table 1**), likely because these groups came from natural populations conditioned by low natural nutrient concentrations. The data reported in Coello-Camba et al. (2014), included communities growing at low nutrient concentrations influencing the value of the maximum growth reported. However, in the experiments run in this study with Arctic communities, nutrient availability was higher (0.62 ± 0.01 μM PO$_4$, 4.25 ± 1.3 μM SiO$_4$, and 8.1 ± 0.49 μM NO$_3$; Boras et al., 2010).

Overall, the average maximum growth rate for the phytoplankton community in the Arctic Ocean was 0.33 (±0.04) d^{-1} and 0.52 (±0.08) d^{-1} in the Southern Ocean. The optimum temperatures were also relatively low (**Table 1**, **Figure 3**). We did not find significant autocorrelations between T_{OPT} and the latitude range covered here.

The T_{OPT} for growth observed for each group ranged between 0 and 14°C (**Table 1**), with average values of 6.4°C (CI$_{90\%}$ = 1.0) of the optimum temperatures for the Arctic phytoplankton community, and 5.5°C (CI$_{90\%}$ = 0.98) for the Southern Ocean. In some cases, when the same phytoplankton group was present

FIGURE 3 | T_{OPT} for phytoplankton growth in polar oceans and latitudinal range of the data. **(A)** Distribution of the optimum temperatures for phytoplankton growth, comparing the data from Thomas et al. (2012) (white) with the dataset obtained in the present work (blue). **(B)** Polar latitudinal range covered in each study.

in different studies, we could observe a more or less wide spread of T_{OPT} between estimations (i.e., Arctic *Phaeocystis* spp., *Micromonas* spp.).

Using this T_{OPT} data and the corresponding maximum growth rates, we estimated the thermal performance curves for Arctic and Southern Ocean phytoplankton communities (**Figure 4**). The three model fits applied to our data resulted in the following formulas (SSE = sum of square errors):

$$h(T) = \frac{ce^{-\frac{0.562}{kT}}}{1 + e^{-\frac{1}{kT}\left(4.1 - \left(0.015 + k\,ln(0.159)\right)T\right)}}, \text{ with SSE } = 0.07;$$

$$h(T) = 0.65e^{\left[-0.5\left(\frac{|T-279.3|}{-5}\right)^2\right]}, \text{ with SSE } = 0.1;$$

$$h(T) = 0.601\left[\frac{T-279.5}{94} + 0.997\right]^{19} e^{-\left[\left(\frac{T-279.5}{94}\right) + 0.997\right]^{20}}$$
$$+ 0.95, \text{ with SSE } = 0.06; \text{ for the}$$
$$\text{Arctic community, and}$$

$$h(T) = \frac{ce^{-\frac{0.549}{kT}}}{1 + e^{\frac{-1}{kT}\left(2.6 - \left(0.009 + kLn(0.268)\right)T\right)}}, \text{ with SSE } = 0.098;$$

$$h(T) = 0.9e^{\left[-0.5\left(\frac{T-278.1}{-6.4}\right)^2\right]}, \text{ with SSE } = 0.093;$$

$$h(T) = 2.548\left[\frac{T-278.3}{176.6} + 0.998\right]^{24} e^{\left[\frac{T-278.3}{176.6} + 0.998\right]^{25}}$$
$$+ 0.960, \text{ with SSE } = 0.109, \text{ for the}$$
$$\text{Southern Ocean community.}$$

This way, the average T_{OPT} for growth obtained here was of 6.5°C (SE = ±0.2) for the Arctic community and 5.2°C (SE = ±0.1) for the Antarctic community.

Activation Energies

Our results showed that E_a was higher at temperatures above the T_{OPT} (fall trait) than below the T_{OPT} (rise trait) (**Figure 1**) in both oceans, with E_a fall values approximately doubling the corresponding E_a rise values (**Figure 5**). The amount of data for the fall traits was scarcer than for the rise traits, particularly for the Southern Ocean. Nonetheless, the differences in E_a derived from each trait were consistent.

Polar Seawater Surface Temperature

Recent (2013, data from http://www.ncdc.noaa.gov) seawater temperatures in the Arctic Ocean are shown in **Figure 6**. In the southernmost Arctic region studied here (70°N), SSTs varied between −1 and 7.2°C during the year. At increasingly higher latitudes, where sea ice is more persistent throughout the year, the temperature gradient became smoother and eventually led to almost stable SSTs (**Figure 6**).

Spring temperatures at the lowest latitudes averaged 0.5°C at 70°N and −0.7°C at 75°N, with a maximum SST of 2.3°C at 70°N. The seasonal warming that takes place during spring became less intense toward the pole, with averaged SSTs of approximately −1.4°C at 80 and −1.7°C at 85°N. During summer, Arctic SSTs averaged 4.9°C at 70°N, 2.1°C at 75°N, −0.4°C at 80°N, and −1.2°C at 85°N, reaching the maximum value in mid-August at 70°N (7.2°C; **Figure 6**).

Arctic SST in 2100

We estimated the seasonal variability of SST in the Arctic Ocean for the end of the twenty-first century with the assumption of a 3°C increase (**Figure 6**) over time. With this warming scenario, seawater temperatures increased at all latitudes, with steeper temperature gradients and strong ice breakup processes at high latitudes. During spring, we estimated SSTs to reach values of
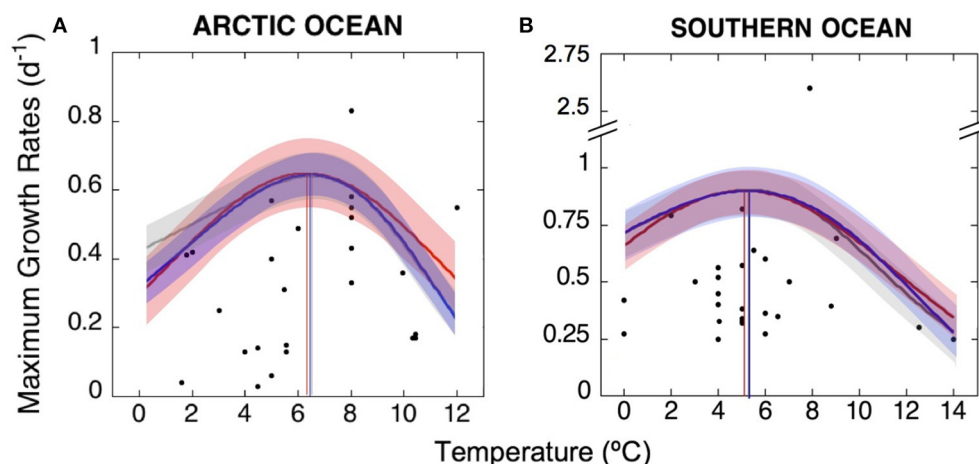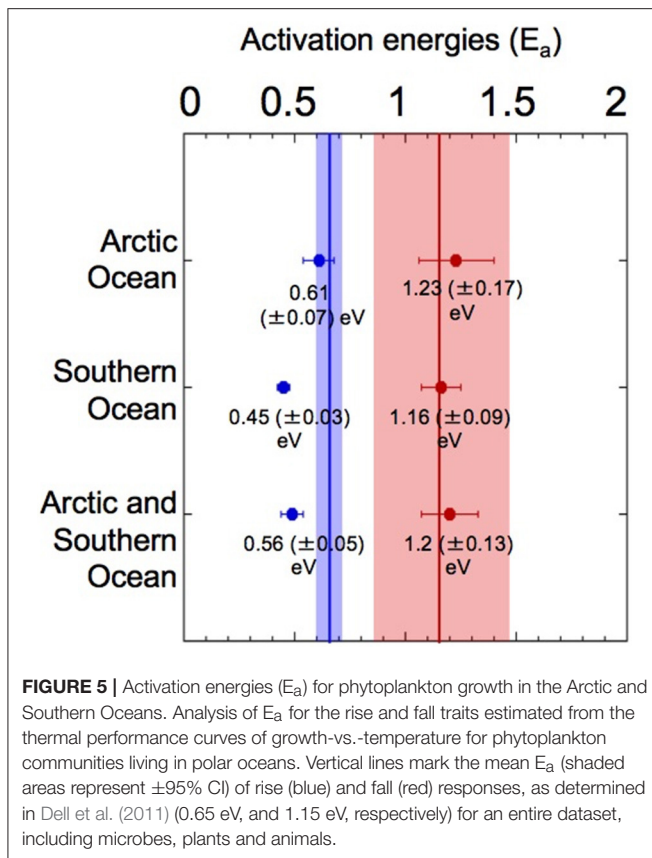

FIGURE 4 | T_{OPT} for growth of Arctic and Antarctic phytoplankton communities. Maximum growth rates observed at the T_{OPT} of phytoplankton species and communities inhabiting **(A)** the Arctic and **(B)** the Southern Ocean, obtained from the literature and new experimental data. We used three fits to better predict T_{OPT} for the whole phytoplankton communities in each polar ocean: gray lines represent the best fit of the Johnson and Lewin model as described by Dell et al. (2011); red and blue curves represent the Gaussian and Weibull functions, respectively, as described by Angilletta (2006). The T_{OPT} calculated by each model were similar and are marked here by vertical lines corresponding to the three fits, which averaged 6.5 ± 0.2°C for the Arctic and 5.2 ± 0.1°C for the Antarctic communities. Shaded areas represent the sum of squared errors (±SSE) of each thermal performance curve.

FIGURE 5 | Activation energies (E_a) for phytoplankton growth in the Arctic and Southern Oceans. Analysis of E_a for the rise and fall traits estimated from the thermal performance curves of growth-vs.-temperature for phytoplankton communities living in polar oceans. Vertical lines mark the mean E_a (shaded areas represent ±95% CI) of rise (blue) and fall (red) responses, as determined in Dell et al. (2011) (0.65 eV, and 1.15 eV, respectively) for an entire dataset, including microbes, plants and animals.

up to 5.2°C at 70°N, 3.4°C at 75°N, 2.1°C at 80°N and 0.7°C at 85°N, toward the end of the century.

During summer, we expect that a higher variation in SSTs will take place at the lowest Arctic latitudes, where maximum SSTs could be as high as 10.2°C at 70°N or 6.5°C at 75°N. Far toward the pole, at 85°N, SSTs may remain above 0°C during this warmest season (**Figure 6**).

DISCUSSION

Our efforts to find studies on optimal temperatures for growth of phytoplankton in polar areas demonstrate that, until now, few datasets describing thermal curves for polar phytoplankton have been published despite their relevance to warming trends currently observed in polar ecosystems. Limitations of the compiled dataset include few temperature treatments, which contributes to uncertainty in the identification of the optimum temperatures for growth in some cases. Moreover, there is a limited number of polar phytoplankton species that have been isolated and successfully cultured in the laboratory, forcing the use of natural communities to test the responses to temperature. This implies that, in some experiments, phytoplankton growth rates could have been constrained due to natural nutrient limitations. Besides this, the geographical distribution of the available data is biased toward some particular regions of the Arctic and Southern Oceans (**Figure 2**). More specifically, most of the Arctic studies on this topic come from the Svalbard

Archipelago (as also pointed by Wassmann et al., 2011), an area influenced by the inflow of the West Spitsbergen Current, and the Canadian Arctic-Baffin Bay area. In the Southern Ocean, most data have been obtained next to the Antarctic Peninsula and the Ross Sea. A seasonal bias can also be found in general in polar research, as the access to study areas is often difficult in the coldest seasons and regions.

Among all the phytoplankton groups studied here, genera such as *Thalassiosira* spp., *Chaetoceros* spp., *Fragilariopsis* spp., and *Phaeocystis* spp. have been usually reported as dominant organisms in the phytoplankton standing stocks associated with spring blooms in the Arctic (Barber et al., 2015). These genera are similar in the Antarctic.

The thermal thresholds determined here do not describe the physiology of these phytoplankton groups, but reflect their ecological preferences. This way, we can depict the actual responses to warming of the phytoplankton groups and autotrophic communities inhabiting polar oceans as a whole. The optimum temperature for growth represents a turning point beyond which temperature becomes a restrictive factor for organisms. By conditioning growth, temperature changes could trigger substantial alterations in phytoplankton responses and therefore in the whole polar ecosystem. The dataset compiled here agrees with the description of Thomas et al. (2012) of lower T_{OPT} for phytoplankton species living at high latitudes (**Figure 3**). We observe that the relatively low T_{OPT} values found (**Table 1**) agree with the low mean annual SST in polar regions: from 1.8°C in the Arctic (Payne et al., 2011) to −0.2°C near the Antarctic Peninsula (Etourneau et al., 2013). For some phytoplankton, T_{OPT} varied between different estimates (i.e., *Micromonas* spp. T_{OPT}: 3.02–8°C). This may suggest that there is genotypic plasticity in responses to temperature that may reflect different adaptations of the strains. This plasticity could be associated with geographical differences of the strains as *Micromonas* showed a higher T_{OPT} in the Canadian Arctic than did the strains from the European Arctic area that showed the lowest values (Lovejoy et al., 2007; Coello-Camba et al., 2015). According to our results, the T_{OPT} estimated for the phytoplankton community from the Southern Ocean (5.2°C) was lower than that estimated for the Arctic phytoplankton community (6.5°C). This difference may be due to the limited connectivity of the polar waters of the Southern Ocean, as the Antarctic Convergence creates an oceanographic barrier that limits exchanges with warmer subpolar areas (Hasle, 1969). This lack of connectivity may result in a higher proportion of cold-adapted species and endemisms (Balech, 1970) that pull the T_{OPT} average down.

The unimodal growth-vs.-temperature curves of both Arctic and Antarctic phytoplankton communities were characterized by left skewness (Dell et al., 2011), as reflected by the higher E_a calculated above than below the optimum (Dell et al., 2011). The E_a values for the fall traits fell within the confidence intervals and were close to the mean value determined by Dell et al. (2011), who performed a global analysis of the thermal E_a of various organisms. The E_a for the rise traits obtained here were low; nevertheless, they agreed with the mean value of 0.50 (±0.18) eV estimated by the same authors for

FIGURE 6 | SSTs and phytoplankton blooms in the Arctic at present and in future scenarios. Arctic phytoplankton blooms (green curves) develop in open waters (wavy dark blue bars) once sea ice retreats (light blue bars). Shaded areas represent daily changes in average SST. **(A)** Recent scenario, temperatures in the Arctic corresponding to 2013 (www.ncdc.noaa.gov) between 70 and 85°N. **(B)** The future SST scenario expected by 2100, assuming a 3°C increase in mean temperatures (right panel) and predicting sharper bloom developments due to faster growth rates at increased temperatures. Black arrows indicate when SSTs increase above the $T_{OPT} = 6.5°C$. Modified after Wassmann and Reigstad (2011) and Leu et al. (2011).

unicellular organisms (Dell et al., 2011). According to this left skewness, phytoplankton living in polar oceans is expected to be more sensitive in responding to increased than to decreased temperatures, as the decrease in the growth rates above T_{OPT} is sharper than the increase in these rates below T_{OPT} (Thomas et al., 2012).

In the Arctic Ocean, summer SSTs have already surpassed the thermal thresholds observed here for phytoplankton. In 2013 at 70°N, temperatures remained above 6.5°C during the first 2 weeks of August, reaching a maximum value of 7.2°C on the 12 August 2013 (**Figure 6**). In contrast, during the last century, temperature increases in the Southern Ocean have been less severe (Christensen et al., 2007), with the highest warming described in the vicinity of the Antarctic Peninsula (Chapman and Walsh, 2007). At present, maximum SSTs in this area (80–50°W, 75°S-Antarctic Convergence) reach up to 4.2°C in January, 1°C below the T_{OPT} for growth that we measured here for Antarctic communities.

Temperature predictions are especially relevant with respect to the Arctic spring bloom, a key process that accounts for the largest part of annual phytoplankton primary production (Lavoie et al., 2009). Leu et al. (2011) presented a conceptual model that described a close coupling between melting ice and primary production in the Arctic Ocean, where pelagic algal blooms require a considerable amount of thinning and broken-up ice. On the basis of Leu's model, Wassmann and Reigstad (2011) added predictions for future Arctic phytoplankton blooms that include earlier bloom development as the ice cover shrinks faster in spring (Wassmann and Reigstad, 2011). Increasing thermal stratification could prevent nutrient supplies during the post-bloom period, softening summer production peaks or even making them disappear (Wassmann and Reigstad, 2011). In addition, in those Arctic regions where strong wind-driven mixing events can weaken the strong vertical stratification, new fall blooms may appear (Ardyna et al., 2014), shifting toward

a double bloom production mode, more typical in temperate waters.

Here we implemented both conceptual models by adding recent seasonal SST variability corresponding to year 2013 (http://www.ncdc.noaa.gov). At present, when spring blooms develop after the ice melts, the average temperature remains below 1°C (**Figure 6**), except at 70°N where there is no ice cover and the main bloom occurs between April and May. At 75°N, a weak and slow surface stratification in spring (Wassmann and Reigstad, 2011) delays the beginning of the bloom by a few weeks. At the heavily ice-covered latitudes of 80 and 85°N, the bloom begins even later in the year, after the ice melts closer to summer. In July 2013, temperatures increased faster at 70°N to a maximum of 7.2°C in August. This seasonal warming became less intense toward the pole, with a maximum SST of −0.4°C at 80°N. Finally, beyond 85°N where sea ice persists throughout the year, the temperature gradient is nearly absent and SST remains stable below −1°C (**Figure 6**).

We estimated the seasonal variability of SST in the Arctic Ocean by 2100 by assuming a 3°C increase over time, a rather conservative prediction taking into account that some regional climate models predict increases of up to 8°C by the end of this century (Collins et al., 2013). As in most future scenarios, our predictions are characterized by steeper temperature gradients with strong ice break-up processes. Predictions indicate that temperature increases would be stronger at the lowest latitudes. Spring temperatures are expected to remain below 1°C at 85°N, while average temperatures would rise higher at 70°N or 75°N as we approach 2100. In fact, throughout the year, conditions at 75°N will be similar to the present-day situation at 70°N, with thermal stratification becoming increasingly stronger at the lowest Arctic latitudes (Leu et al., 2011; Wassmann and Reigstad, 2011). Besides this, predicted SSTs at 70°N are expected to exceed the T_{OPT} all summer long by the end of this century and during the first half of August at 75°N.

As the seasonal ice melts, temperatures will increase more abruptly, although our predictions for 2100 do not anticipate that SST will exceed the T_{OPT} of Arctic phytoplankton growth in spring (**Figure 6**) when the bloom for primary production begins. Nonetheless, increased temperatures may lead to subsequent increases in the growth rates of phytoplankton (**Figures 4**, **5**), resulting in a fast increase in blooming biomass. As a consequence, nutrient consumption may also be accelerated, giving way to a more rapid decrease at the end of the bloom (**Figure 6**). However, under this low emission future forecast, we expect that the T_{OPT} threshold would not be exceeded in spring. Polar phytoplankton species should therefore be able to grow properly and dominate the spring blooms (**Figure 6**). If we also consider the predicted increase in pCO_2 by 2100 (Meehl et al., 2007), the acceleration of the Arctic spring bloom could be even larger as a consequence of the fertilizing effect of pCO_2. This could compensate present pCO_2 limitation in those areas where nutrients are still available and temperatures remain below 6°C (Holding et al., 2015). This dependence of the fertilizing effect of increased pCO_2 on temperature adds to the temperature threshold of 6.5°C predicted here for the growth of Arctic phytoplankton communities.

As the temperature of polar seawater increases, the principle of competitive exclusion implies that more thermo-tolerant phytoplankton groups (i.e., species or ecotypes) would out compete cold-water phytoplankton groups with lower growth T_{OPT} in polar waters. Some phytoplankton species can exhibit phenotypic plasticity to temperature (Reusch and Boyd, 2013). Among cold-water communities, extremely low temperatures have forced specific cellular and physiological adaptations (Morgan-Kiss et al., 2006). Phytoplankton can adapt to temperature under stable conditions (Huertas et al., 2011). The low interannual variability in temperature of these extremely cold niches has helped that adaptation but environmental increases in temperature above the regular values is limiting the capacity of low-temperature phototrophs to adapt to large increases in SSTs (Morgan-Kiss et al., 2006; Bonebrake and Mastrandrea, 2010; Huertas et al., 2011). This way, under future increased temperatures, a compositional change of communities from less to more thermo-tolerant groups rather than local adaptive evolution would be expected.

According to this principle, once seawater temperatures in a warmer polar ocean surpass the T_{OPT} of resident communities, these high-latitude niches will be opened up for incoming subpolar temperature-tolerant species. However, studies addressing the plasticity of phytoplankton species in polar waters to temperature changes are still limited, so predictions on community changes remain a challenge. Nonetheless, toward the end of this century, SSTs are expected to remain low during winter, with ice formation (Serreze et al., 2007) and limited light availability for primary production (Berge et al., 2015). Under these unfavorable conditions, many polar phototrophic plankton are able to persist by following different strategies such as facultative heterotrophy, storage and utilization of energy reserves at a reduced metabolic rate and formation of resting spores (Palmisano and Sullivan, 1982; Zhang et al., 1998). Incoming temperate species may not have the potential to survive

such long periods of darkness (Peters, 1996; Peters and Thomas, 1996), and thus there are uncertainties in predicting their ability to offset polar species during the polar night. Polar species may then retain a competitive advantage surviving during the coldest months, and they will likely maintain their key role in seeding the subsequent spring polar bloom, as long as their optimum temperature for growth is not exceeded in spring. The income of subpolar phytoplankton species is more likely to happen in the Arctic Ocean, where advection processes help in connecting the polar ocean with waters at lower latitudes. Increased temperatures would favor the growth of the newly arriving groups that are already adapted to higher temperatures. In the Southern Ocean, atmospheric and oceanic patterns result in higher isolation (Hunt et al., 2016). This way, Southern Ocean phytoplankton communities might live in a narrower environmental temperature range, but they are less influenced by the influx of species from lower latitudes.

Future predictions describe a longer ice-free period in the Arctic Ocean and in some areas of the Southern Ocean, where ice will melt faster in spring and consequently make phytoplankton blooms begin earlier. According to our results, we expect that warming may lead to more intense but shorter spring bloom peaks in the Arctic Ocean. These alterations in the timing of blooms and ultimately in food quality could disrupt the delicate balance among trophic levels (Søreide et al., 2010) with implications for polar trophodynamics (Boyd et al., 2013).

The thermal threshold defined here for Arctic communities is already exceeded in August at the lowest Arctic latitudes. In future scenarios, this potential threat to phytoplankton will affect increasingly higher latitudes and move closer to the blooming season, extending into July and September. In fact, if we consider the RCP8.5 high-emission scenario described in the 2013 IPCC report, we can expect the T_{OPT} to be exceeded in spring at 70°N before reaching the year 2100. The literature on species thermal performance suggests that once the T_{OPT} is exceeded, the growth of organisms is constrained. Instead, if we consider a low-emission scenario, an intense increase in spring SST is not expected to take place during this century.

At present, polar studies are still quantitatively and geographically restricted, likely constraining our comprehension of the effects of global warming in polar oceans. Also, the temperature range of some of the growth-vs.-temperature curves included in this study were not wide enough to properly accommodate the optimum value, and nutrient limitation could constrain the growth results from some experiments. We highlight the importance of an increase in the number of species studied from the polar areas. More investigation is required to understand how predicted changes in environmental factors such as temperature, as addressed here, may influence polar phytoplankton in the decades to come.

AUTHOR CONTRIBUTIONS

AC and SA were responsible for running all experiments, collecting data from the literature, performing data analysis and for writing and editing the manuscript.

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