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Temperature thresholds for Arctic plankton community metabolism: an experimental assessment

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Abstract

Climate warming is especially severe in the Arctic, where the average temperature is increasing 0.4 °C per decade, two to three times higher than the global average rate. Furthermore, the Arctic has lost more than half its summer ice extent since 1980 and predictions suggest that the Arctic will be ice free in the summer as early as 2050, which could increase rate of warming. Predictions based on the metabolic theory of ecology assume that temperature increase will enhance metabolic rates and thus both the rate of primary production and respiration will increase. However, these predictions do not consider the specific metabolic balance of the communities. We tested experimentally the response of Arctic plankton communities to seawater temperature spanning from 1 °C to 10 °C. Two types of communities were tested, open-ocean Arctic communities from water collected in the Barents Sea and Atlantic influenced fjord communities from water collected in the Svalbard fjord system. Metabolic rates did indeed increase as suggested by metabolic theory, however these results suggest a temperature threshold of 5 °C, beyond which the metabolism of plankton communities shifts from autotrophic to heterotrophic. Barents Sea communities showed a much clearer threshold response to temperature manipulations than fjord communities.

1 Introduction

The Barents sea region of the Arctic Ocean is highly influenced by the North Atlantic Current which brings warm waters into the Arctic causing it to be a relatively ice free area and contributing significantly to summer ice melt (Loeng et al., 1997; Schauer et al., 2002). These physical properties are responsible for the high CO_2 uptake in the mostly ice-free Barents Sea, which is estimated to be 9×10^{12} g C yr^{-1} (Fransson et al., 2001), compared to the entire ice-covered Arctic interior (31×10^{12} g C yr^{-1}; Katlin and Anderson 2005). This relatively high CO_2 sinking capability is owed in part to the high biological production in this area (Loeng et al., 2005). The European Arctic Corridor, including the Barents Sea, is responsible for about 50 % of the primary production in the entire Arctic Ocean (Sakshaug, 2004; Ellingsen et al., 2008; Pabi et al., 2008) which has been estimated to have primary production rates between < 30–$> 100\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ depending on the mixing properties and ice cover of the region (Wassmann et al., 2010). High primary production supports productive fisheries (Pauly and Christensen, 1995) and contributes to the high atmospheric CO_2 uptake in the North Atlantic (Takahashi et al., 2002).

Yet, the Arctic region is experiencing rapid climate change, warming three times faster than the global mean (ACIA, 2004; Trenberth et al., 2007). Such a steep rate of warming has resulted in severe reduction in ice cover, exceeding the range of natural variability over the past millennia and creating potentially dangerous positive feedbacks (Walsh, 2008; Duarte et al., 2011). Rapid warming is expected to continue in the future, with up to 6 °C warming throughout the 21st century (ACIA, 2004), and revised forecasts suggest that the Arctic will be ice free in the summer before 2050 (Holland et al., 2006; Boé et al., 2009; Wang and Overland, 2009; Wadhams, 2011) The ice cover over the Arctic Ocean reached a historical minimum in September 2007 with a reduction of 43 % relative to the ice cover in 1979 (Kerr, 2007). In 2011 ice cover again approached this historical minimum (National Snow and Ice Data Center, nsidc.org). Sea ice is not only changing in extent, but is also decreasing in thickness (Johannessen et al., 1999; Kwok and Rothrock, 2009; Wadhams, 2012) and increasing in duration of the ice melt season (Belchansky et al., 2004). These factors are expected to affect the primary productivity in the region by changing light regimes or affecting the timing of the spring bloom (Wassmann et al., 2006, 2008, 2010; Ellingsen et al., 2008). Indeed, previous studies have reported an increase in primary productivity for the Arctic as a whole for these reasons (Arrigo et al., 2008; Pabi et al., 2008), however closer inspection actually reveals a decline in primary production in the Greenland and Barents Seas in 2007 due to increased ice-cover moving out of the Arctic's interior (Wassmann et al., 2010).

Besides light availability, temperature also plays a major role in regulating metabolic processes (Iriberri et al., 1985; White et al., 1991; Brown et al., 2004), as described by the Metabolic Theory of Ecology (MTE; Brown et al., 2004), which predicts that primary production and respiration rates should increase at different rates with increasing temperature (Harris et al., 2006; Lopez-Urrutia et al., 2006). Noting that metabolic theory predicts that the activation energy for respiration should be twice as high as that for photosynthesis, Harris et al. (2006) predicted that a four degree increase in water temperatures should result in a 20 % increase in net primary production and a 43 % increase in heterotrophic metabolism, resulting in a 16 % decrease of the Photosynthesis/Respiration ratios (P/R). Moreover, there is evidence that respiration rates show very steep responses to increased temperature at the low ambient temperatures found in Arctic waters (Pomeroy and Wiebe, 2001; Vaquer-Suyner et al., 2010). Indeed, the mean activation energy for community respiration in the Greenland Sea, derived from 13 independent experiments, has been reported to be 1.05 ± 0.3 eV (Vaquer-Suyner et al., 2010), well above the value of 0.65 eV predicted from theory (López-Urrutia et al., 2006). On the basis of these results, Vaquer-Suyner et al. (2010) postulated that warming may lead to Arctic communities shifting from acting as an intense sink for atmospheric CO_2, as they do at present, to become CO_2 sources to the atmosphere, due to enhanced respiration rates, and suggest that this shift may occur within 6 °C of warming, with consequences for the global carbon budget and climate (Duarte et al., 2011).

Here we test the hypothesis (Vaquer-Suyner et al., 2010; Duarte et al., 2011) that Arctic plankton communities shift from acting as CO_2 sinks to acting as CO_2 sources at a temperature threshold within 6 °C of current temperatures. We do so through an experimental examination of the temperature-dependence of response of Arctic community metabolism along the temperature range of 1 to 10 °C, encompassing the range of seawater temperature expected for the Arctic Ocean along the 21st Century (ACIA, 2004). To examine the possible role of temperature acclimation and adaptation of the communities, two separate experiments were conducted, one with a plankton community sampled in the Arctic water close to the marginal ice zone of the Barents Sea and an experiment with a community collected in warmer, Atlantic-influenced fjords.

2 Methods

2.1 Experiment with a Barents Sea community

We designed the experiments to compare the responses of an open-ocean Arctic community and an Arctic community already acclimated to warm temperatures. We were conscious of the limitations of experimental manipulations to simulate changes, such as their short temporal scales that do not allow for genetic changes and community restructuring to occur as well as the risk of creating a "shock" treatment resulting in unexpected responses. To rectify these concerns, rather than examine instantaneous responses to warming, we allowed the communities to adjust to the experimentally-imposed temperature regime, by incubating the mesocosms containing the communities for 10 to 15 days, imposing warming rates (°C day^{-1}) comparable to those observed in nature, thereby allowing the responses to be expressed. Hence, the responses evaluated here have two components (1) a physiological component, reflecting the effect of temperature on metabolic processes; and (2) a community component, reflecting the effect of temperature on community composition and biomass.

Seawater samples were collected in 60 l polypropylene carboys previously treated with HCl for at least 48 h and thoroughly rinsed with the seawater from the sampling site. The experimental evaluation of temperature effects on the community metabolism of an open-sea planktonic community was performed with the plankton community found in water collected on 27 June 2009 at 26 m depth in the Barents Sea, South East of the Svalbard archipelago, using the CTD rosette sampling system available on R/V Jan Mayen (water temperature −1.19 °C, salinity 33.92; Fig. 1). A second experiment was conducted using fjord water sampled from a boat using a pump at 2 m depth in Isfjorden, the second largest fjord in Svalbard (Fig. 1). In contrast to the first experiment with the Barents Sea plankton community, the community sampled at Isfjorden was expected to represent an Atlantic-influenced community growing at warmer temperatures, thereby assessing the responses of both Arctic communities and the Atlantic community expected to invade an Arctic Polar Ocean free of ice. Indeed, water temperature at Isfjorden (6.2 °C) on the sampling date (8 July 2009) was much higher than that of the Barents Sea community, whereas the salinity was comparable (32.73).

2.2 Experimental design and set-up

The experiments were conducted in cold, temperature regulated chambers (set at 4–5 °C) at the University Center in Svalbard (UNIS), Longyearbyen. All plastic and glassware used for the incubations was previously cleaned with HCl and thoroughly rinsed with seawater. Seven experimental temperatures, ranging from 1.5 °C to 10.5 °C, in 1.5 °C increments, were tested, thereby encompassing the full range of temperatures forecasted for the Arctic over the 21st Century. The water from the 60 l carboys was mixed in 280 l containers and transferred to duplicate acid-washed 20 l polycarbonate bottles. The duplicate bottles for each experimental temperature were submersed in 280 l tanks connected to a temperature control unit (precision ±0.1 °C) with an impelling and expelling pump. Temperature data loggers were submersed in each tank to monitor the resulting water temperature. The setup was completed with two fluorescent light tubes per tank as to provide an appropriate, continuous light environment.

The temperature treatments for the Barents Sea community, sampled at −1 °C in situ temperature, were achieved by gradually warming over three days to reach the target temperature while avoiding a temperature shock response of the communities. We did not raise the temperature gradually for the fjord community as the water was collected at 6.2 °C. Due to the unstable temperature conditions in the cooling rooms, the temperatures fluctuated somewhat along both experiments, but the average temperature was successfully maintained in the different tanks (Tables 1 and 2). The experiment was maintained during 15 days for the Barents Sea community and 10 days for the Isfjorden community. The Arctic community was maintained longer due to a slower response time, which was determined using daily chlorophyll-*a* measurements to evaluate the time-course of the response. The duplicate samples for the Barents sea community were pooled after day 10 to have sufficient water volume to continue the experiment on to day 15. The 7 °C temperature treatment was lost in the middle of the experiment with the Isfjorden community due to technical problems leading to a sharp increase in temperature. Hence, this treatment was discontinued.

Samples of 50 ml for chlorophyll-*a* determination were collected daily and filtered through Whatmann GF/F filters. Chlorophyll-*a* on the filters was extracted in 90 % acetone for 24 h. The concentration was measured fluorometrically following Parsons et al. (1984).

Community metabolism (gross primary production, community respiration and net community production) was determined from changes in oxygen over a 24 h period. During the experiment with the Arctic community, metabolism was sampled once on the first day for only one of each the duplicate replicates, 2 complete times in each replicate mesocosm, and a forth time in after duplicate replicates were pooled. Isfjorden Communities were sampled twice in each of the replicate mesocosm. Water samples from each of the 14 experimental units were carefully siphoned into narrow-mouth 25–35 ml Winkler bottles. Five replicates were used to determine the initial oxygen concentration, and five replicates bottles were incubated for 24 h in both the “dark” and “light” in the temperature tanks from where the sample was taken. Net community production (NCP) and community respiration (CR) were measured by monitoring oxygen concentration changes in the light and dark bottles along the incubation (Carpenter, 1965; Carritt and Carpenter, 1966). Oxygen concentrations were analyzed by Winkler titration using a potentiometric electrode and automated endpoint detection (Mettler Toledo, DL28 titrator) following Oudot et al. (1988). CR and NCP were calculated from changes in dissolved oxygen concentration from the initial concentration measured after incubation of samples under “dark” and “light” conditions, respectively and gross primary production (GPP) was calculated by solving the mass balance equation $\mathrm{GPP} = \mathrm{NCP} + \mathrm{CR}$.

3 Results

3.1 Response of the Barents Sea community

The Barents Sea community showed a significant decline in chlorophyll-*a* concentrations along the temperature range (Fig. 2), as described by a fitted regression equation with a slope of $-0.02\,\mu\text{g Chl-}a\,\text{l}^{-1}$ ($R^2 = 0.68$, $p = 0.02$) using mean chlorophyll-*a* concentrations for all days sampled.

Community metabolism rates fluctuated greatly throughout the time course of the experiment, as expected as the communities adapted to their new temperature treatments. Most notable differences in temperature treatments took place in the last measurement with pooled mesocosms at day 15 (Fig. 3a–c), as clear difference in chlorophyll-*a* concentrations began to be seen (Fig. 3a). CR for the lowest temperatures (1.5, 3 and 4.5 °C) remained low throughout the experiment, while CR for medium temperatures (6 and 7.5 °C) rose throughout reaching their highest rates at day 15 (Fig. 3b). CR for 9 °C appeared to respond positively at day 9, but further incubation resulted in a low CR at day 15. CR for the 10.5 °C treatment decreased throughout the time course (Fig. 3b). Patterns for NCP show similar patters across treatments throughout the time course of the experiment however increasing differences began to emerge as time increased resulting in highest NCP for the 3, 4.5 and 10.5 °C treatments (Fig. 3c) at day 15. These treatments also resulted in autotrophic communities (i.e. where $\text{NCP} > 0$; Fig. 3c) by day 15.

When measured initially, the replicates of the Barents Sea plankton community samples were different, with one replicate acting strongly heterotrophic (i.e. $\text{NCP} < 0$; $\text{NCP} \pm \text{SE} = -9.31 \pm 0.10$) and the other acting autotrophic (i.e. $\text{NCP} > 0$; $\text{NCP} \pm \text{SE} = 4.41 \pm 0.18$). Through the rest of the experiment there was no noticeable difference between the replicates so further analysis was carried out averaging the replicates together. Community respiration (CR) showed a variable response to experimental temperature increase with mean CR rates (±SE). Rates remained low for the lower temperatures tested while reaching their highest CR rate at an intermediate temperature of

5.8 °C and declining somewhat with additional warming (Fig. 4a; Table 1). Net community metabolism was balanced across the experiment (i.e. $H_o: NCP = 0$, t-test, $p = 0.41$) at low temperatures, but the community became net heterotrophic ($NCP < 0$, $CR > GPP$) at temperatures above 4.2 °C (Fig. 4c; Table 1). The temperature-dependence of NCP was driven by changes in CR, since GPP was variable and independent of temperature changes ($p = 0.50$; Fig. 4b; Table 1).

Since chlorophyll-*a* concentrations declined across temperature treatments (Fig. 2), the responses in community metabolism may reflect changes in community biomass rather than physiological responses forced by temperature treatments. Hence, we examined the response of metabolic rates standardized to chlorophyll-*a* concentrations measured in each mesocosm on the same sampling day in an attempt to extract any physiological signal from the community responses. Indeed, CR rates standardized per unit chlorophyll increased significantly with increasing temperature ($R^2 = 0.64$, $p = 0.03$). However, inspection of the relationship between CR per unit chlorophyll and experimental temperature suggested that the relationship was best modeled as a logistic relationship (Fig. 5). Indeed, the changes in CR per unit chlorophyll with temperature was well described by a logistic regression characterized by low CR per unit chlorophyll-*a* at low temperatures ($3.75 \pm 0.90\ \mu mol\ O_2\ \mu g\ Chl\text{-}a^{-1}\ day^{-1}$) and an abrupt increase, to double the rates ($7.71 \pm 0.74\ \mu mol\ O_2\ \mu g\ Chl\text{-}a^{-1}\ day^{-1}$), beyond a mean (±SE) threshold temperature of 5.06 ± 3.02 °C ($R^2 = 0.84$, $p = 0.19$; Fig. 5).

Specific GPP rates, standardized per unit biomass also showed a lot of variation. Mean (±SE) specific GPP rates per unit chlorophyll-*a* ranged between $4.14 \pm 0.86\ \mu mol\ O_2\ \mu g\ Chl\text{-}a^{-1}\ day^{-1}$ at 2.6 °C and $1.37 \pm 0.69\ \mu mol\ O_2\ \mu g\ Chl\text{-}a^{-1}\ day^{-1}$ at 7.8 °C, without any clear relationship with the experimental temperature (Table 1). Thus, the specific NCP per unit chlorophyll-*a* was also driven by changes in CR and, therefore, also showed a logistic relationship with experimental temperature (Fig. 6) with a mean (±SE) threshold temperature at 4.78 ± 1.26 °C ($R^2 = 0.78$, $p = 0.032$; Fig. 6) with a mean (±SE) specific NCP rate at colder temperature of $-0.72 \pm 1.31\ \mu mol\ O_2\ \mu g\ Chl\text{-}a^{-1}\ day^{-1}$, indicative of balanced metabolism, and a strongly heterotrophic community with mean (±SE) specific NCP of $-5.52 \pm 1.05\,\mu$mol O_2 µg Chl-*a*$^{-1}$ day^{-1} developing at warmer temperatures (Table 1; Fig. 6).

3.2 Atlantic-influence fjord water community

Atlantic community showed no significant trend in chlorophyll-*a* concentrations along the experimental temperature range (Fig. 7) with the highest mean biomass of about 1.5 µg Chl-*a* l^{-1} developed at the temperature at which the sampled community was growing of 6.2 °C (Table 2). Atlantic communities were originally close to being balanced (NCP ±SE $= -0.73 \pm 0.35$) while specific community metabolic rates were heterotrophic (NCP ± SE $= -3.49 \pm 1.65$). Community respiration (CR) for the Atlantic influenced community showed high variation and no clear relationship with experimental temperature, similar to gross primary production (Table 2), and net community. As a consequence, net community production was independent of experimental temperature, with some temperature treatments (i.e. 3 and 8.5 °C) resulting in strong heterotrophic community metabolism (Table 2).

Since chlorophyll-*a* concentrations were independent of the experimental temperature, the chlorophyll-*a* specific rates showed the same patterns as those of the volumetric rates, with no significant relationship with the experimental temperature (Table 2).

4 Discussion

The experimental results presented show that the metabolism of the open-sea Arctic community collected in the Barents Sea was highly sensitive to warming, whereas that of the community already growing in the Atlantic-influenced, warm-water Arctic fjord, showed no clear relationship with experimental temperature across the 1 to 10 °C experimental range.

Consistent with predictions from metabolic theory (Harris et al., 2006; Lopez-Urrutia et al., 2006) and short-term experiments (Vaquer-Sunyer et al., 2010), experimentally increased water temperature in the Barents Sea plankton community resulted in a shift from balanced metabolism (NCP = 0, GPP = CR) at lower temperatures to a strongly heterotrophic community (NCP < 0, GPP < CR), acting as a CO_2 source. This response was, however, steeper than expected. Whereas the expectations derived from the consideration of the temperature-dependence of metabolic processes (Harris et al., 2006; Lopez-Urrutia et al., 2006; Vaquer-Sunyer et al., 2010), the realized responses involved also changes at the community level, particularly a decline in chlorophyll-*a* concentration. Moreover, the decline in chlorophyll-*a* concentration with increasing temperature explains that, unlike the predictions by metabolic theory, gross primary production did not show significant increase with warming for the Barents Sea community, despite a tendency for increased chlorophyll-*a*-specific GPP at higher temperatures (Table 1). Hence, the increase in CR and decline in NCP for the Barents Sea community with increasing warming compounded physiology-level with community-level responses to yield a much steeper decline in net community metabolism of the community, which becomes strongly heterotrophic. Previous examinations of the temperature-dependence of community metabolism, available only for respiration rates, used short-term, 24 h to 48 h, experiments (Vaquer-Sunyer et al., 2010), and did not allow, therefore, for responses in community structure to be realized.

Using the Van't Hoff-Arrhenius relation, we can then estimate the activation energy (E_i) required for the reaction of respiration across experimental temperature treatments using the equation: $B \sim e^{-Ei/kT}$ and the Boltzman's constant, k (8.617343×10^{-5} eV K^{-1}), where B is the metabolic rate and T the temperature in Kelvin (Gillooly et al., 2001; Brown et al., 2004). The experiment conducted with the Barents Sea community yields an E_i of approximately 0.85 eV, higher than the value of 0.65 eV predicted from theory (López-Urrutia et al., 2006), but not different from E_i derived from short-term experiments of 1.05 ± 0.3 eV (Vaquer-Suyner et al., 2010). The E_i of 0.85 eV derived here confirms that respiration rates of Arctic plankton communities have E_i values above the rate of 0.41–0.74 eV suggested for organisms living at intermediate temperature regimes (Gillooly et al., 2001; Brown et al., 2004). This finding confirms the conclusion that the respiration of planktonic communities organisms growing at the lower range of ocean temperature show a steep response to increased temperature (Pomeroy and Wiebe, 2001; Vaquer-Suyner et al., 2010). In contrast, this could also be the reason that no significant relationships were found in the experiment with the Atlantic-influenced fjord water communities, which are exposed to much more variable temperatures throughout the spring melt season.

Most importantly, the results obtained here allowed the postulated temperature threshold beyond which Arctic communities become heterotrophic to be experimentally resolved at about 5 °C (4.78 ± 1.26 °C). Indeed, the relationship between net community metabolism and temperature was best described as a logistic relationship where communities shift from metabolic balance to net heterotrophic beyond a temperature threshold of 5 °C, above which the specific community respiration doubles and NCP is reduced 5-fold. These results provide, therefore, support for the proposition that Arctic plankton community metabolism shows tipping point behavior (Duarte et al., 2011), and quantifies the tipping point for the community to flip from acting as a CO_2 sink to a CO_2 source at a temperature threshold of 5 °C. Isfjorden communities were growing in Arctic ecosystems invaded by warm Atlantic waters, however decreasing water temperature did not cause the metabolic rates of the Isfjorden community tested here to become autotrophic, within the limitations of the duration of the experiment conducted here. This may suggest the presence of hysteresis creating a resistance for communities already growing in warm waters to revert from a net heterotrophic community to an autotrophic one as waters become colder (Duarte et al., 2011).

The results here derive from mesocosm experiments and therefore suffer from the limitations inherent to these experimental set-ups (cf. Duarte et al., 1997). However, the results do not stand alone in concluding that polar plankton communities show a steep response to warming, as these results are supported by theoretical expectations (Harris et al., 2006; López-Urrutia et al., 2006; Duarte et al., 2011) and short-term warming experiments in polar communities (Pomeroy and Wiebe, 2001; Vaquer-Suyner et al., 2010). Warming leads to a steep increase in respiration rates of polar plankton communities. The Arctic community is, however, more vulnerable to warming than that of Southern Ocean communities, as Arctic communities have access to large pools of dissolved organic carbon that lead to high community respiration rates and allow net heterotrophic communities to prevail (Regaudie-de-Gioux and Duarte, 2010). The present results suggest that Arctic plankton communities may be considered, as proposed by Duarte et al. (2011), as tipping elements (sensu Lenton et al., 2008), triggering changes when perturbed beyond climatic tipping points. Specifically, an increase beyond 5 °C in the Arctic Ocean could lead plankton communities to become strongly heterotrophic in the Arctic summer, leading to a shift of the Arctic Ocean region from a large sink of atmospheric CO_2 (Takahashi et al., 2002) to a CO_2 source with further future climate warming.

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Table 1. Experiment with Arctic open-water community. Average temperature (±SE), Chlorophyll-*a* (±SE), and volumetric and specific NCP, CR and GPP rates (±SE) over 15 days of experimental treatment including initial measurements (t0).

Temperature (°C)	Chl-*a*	NCP		CR		GPP		GPP/CR
	µg l^{-1}	Volumetric µmol O_2 l^{-1} day^{-1}	Specific µmol O_2 µg Chl-a^{-1} day^{-1}	Volumetric µmol O_2 l^{-1} day^{-1}	Specific µmol O_2 µg Chl-a^{-1} day^{-1}	Volumetric µmol O_2 l^{-1} day^{-1}	Specific µmol O_2 µg Chl-a^{-1} day^{-1}	
t0	1.00 ± 0.16	−2.45 ± 6.86	−3.64 ± 7.43	7.18 ± 6.98	8.50 ± 8.33	4.73 ± 0.11	4.87 ± 0.90	11.58 ± 11.24
1.72 ± 0.26	0.72 ± 0.06	−0.94 ± 1.40	−0.98 ± 1.95	1.90 ± 0.31	2.74 ± 0.57	0.70*	2.06*	0.52*
2.60 ± 0.5	0.63 ± 0.08	0.20 ± 1.43	−0.59 ± 2.35	2.65 ± 0.31	5.02 ± 1.39	2.78 ± 0.99	4.14 ± 0.86	1.31 ± 0.64
4.15 ± 0.06	0.70 ± 0.06	−0.28 ± 0.95	−1.34 ± 1.70	2.08 ± 0.62	3.54 ± 1.29	1.69 ± 0.05	2.17 ± 0.11	1.20 ± 0.39
5.76 ± 0.10	0.76 ± 0.078	−3.86 ± 0.93	−5.53 ± 1.37	5.37 ± 1.15	7.68 ± 1.45	2.13 ± 0.69	3.01 ± 0.92	0.40 ± 0.16
7.77 ± 0.15	0.55 ± 0.04	−3.87 ± 0.69	−7.22 ± 1.85	4.01 ± 0.66	7.16 ± 1.52	0.81 ± 0.36	1.37 ± 0.69	0.19 ± 0.08
8.53 ± 0.05	0.48 ± 0.05	−2.81 ± 0.97	−6.07 ± 1.83	4.14 ± 1.32	8.88 ± 2.16	1.75 ± 0.47	3.52 ± 0.65	0.41 ± 0.10
10.42 ± 0.23	0.462 ± 0.06	−1.74 ± 0.86	−2.99 ± 2.06	3.14 ± 0.91	7.00 ± 0.89	0.98 ± 0.38	4.01 ± 2.78	0.61 ± 0.39

[*] Signifies number with out SE due to lack of viable replicates.

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Thresholds for Arctic plankton metabolism

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Table 2. Experiment with Atlantic influenced fjord communities. Average temperature (±SE), Chlorophyll-*a* (±SE), and volumetric and specific NCP, CR and GPP rates (±SE) over 10 days of experimental treatment including initial measurements (t0).

Temperature (°C)	Chl-*a*	NCP		CR		GPP		GPP/CR
	μg l^{-1}	Volumetric µmol O_2 l^{-1} day^{-1}	Specific µmol O_2 µg Chl-*a*$^{-1}$ day^{-1}	Volumetric µmol O_2 l^{-1} day^{-1}	Specific µmol O_2 µg Chl-*a*$^{-1}$ day^{-1}	Volumetric µmol O_2 l^{-1} day^{-1}	Specific µmol O_2 µg Chl-*a*$^{-1}$ day^{-1}	
t0	0.21 ± 0.002	0.73 ± 0.35	−3.49 ± 1.65	1.79*	8.61*	1.41*	6.78*	0.79*
1.11 ± 0.01	1.07 ± 0.34	2.78 ± 4.19	6.27 ± 9.26	1.59 ± 0.61	1.45 ± 0.25	3.93*	2.14*	1.78*
2.86 ± 0.06	1.19 ± 0.38	−1.56 ± 1.89	−3.59 ± 3.80	6.14 ± 0.85	7.16 ± 2.69	4.58 ± 1.75	3.57 ± 1.30	0.79 ± 0.26
4.03 ± 0.05	1.28 ± 0.39	2.07 ± 4.11	5.94 ± 6.95	5.27 ± 0.34	4.57 ± 1.98	3.29 ± 1.30	3.58 ± 2.51	0.60 ± 0.22
5.48 ± 0.03	1.58 ± 0.45	0.37 ± 1.73	1.22 ± 1.39	5.21 ± 1.21	3.06 ± 0.45	4.22 ± 1.05	3.04 ± 1.19	0.10 ± 0.86
8.33 ± 0.11	1.54 ± 0.47	−5.24 ± 5.51	−1.78 ± 2.59	9.02 ± 6.69	4.31 ± 2.66	1.44 ± 0.41	1.14 ± 0.58	0.62 ± 0.34
9.92 ± 0.05	0.94 ± 0.23	1.14 ± 2.10	3.44 ± 3.11	2.34 ± 1.36	1.86 ± 0.87	3.48 ± 1.15	5.29 ± 2.37	10.74 ± 6.76

* Signifies number with out SE due to lack of viable replicates.

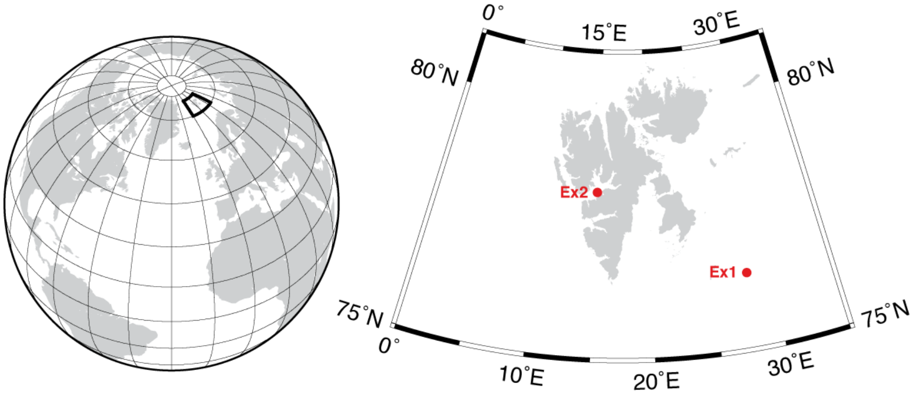

Fig. 1. Location where the Arctic communities used in the experiments were sampled. Ex1 refers to the location in the Barents Sea of the open-sea Arctic plankton community, while Ex2 shows the location of the Atlantic-influenced, Isfjorden plankton community.

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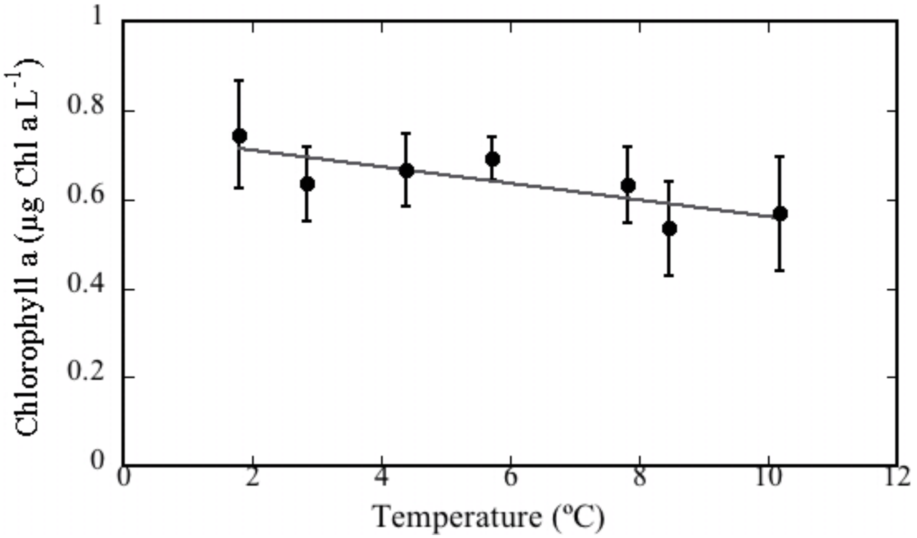

Fig. 2. Mean (±SE) chlorophyll-*a* concentration (µg Chl-*a* l^{-1}) of the Barents Sea plankton community tested here, averaged over the days when samples for determination of metabolic rates were taken, versus the mean temperature (°C) recorded for each experimental treatment. The solid line shows a significant ($p = 0.02$) decrease in chlorophyll-*a* concentration with temperature ($R^2 = 0.68$).

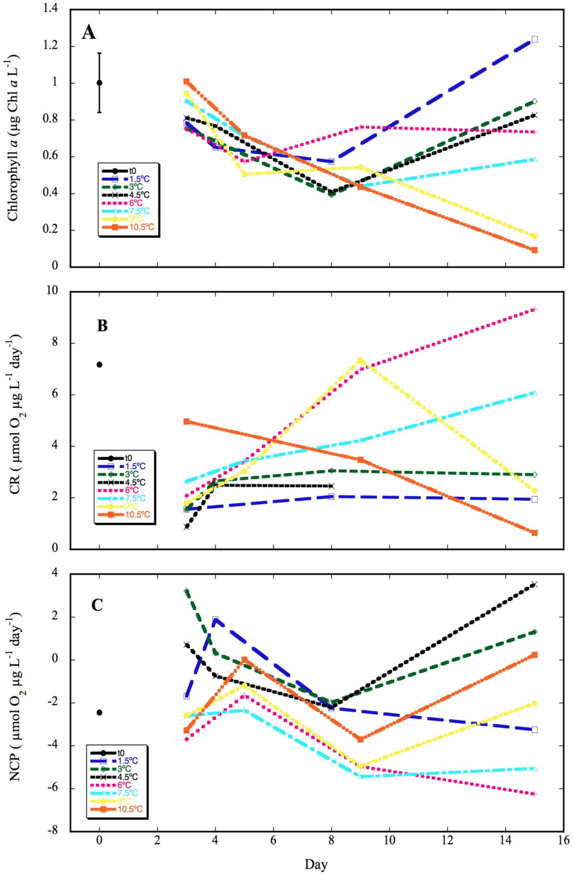

Fig. 3. Representation of the time course of mean biomass **(a)** mean CR rate **(b)** and mean NCP rate **(c)** of Barents Sea plankton community throughout 15 days of experiment treatment. Colors represent different temperature treatments.

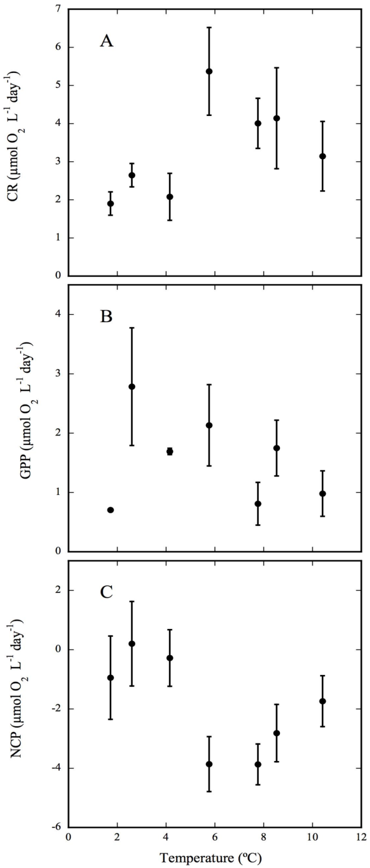

Fig. 4. Barents Sea plankton community mean (±SE) volumetric community metabolic rates: CR **(a)**, GPP **(b)**, and NCP **(c)** averaged over the days when samples for determination of metabolic rates were taken, versus the mean temperature (°C) recorded for each experimental treatment.

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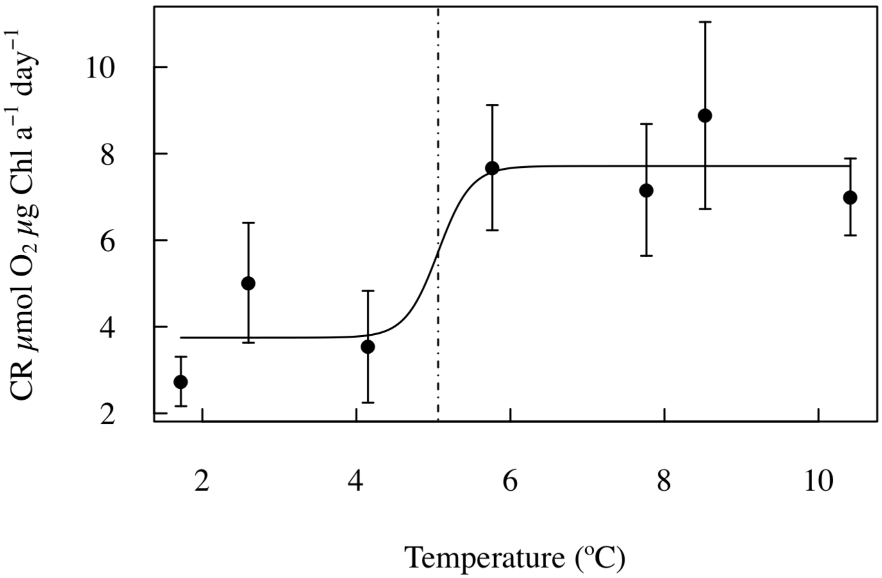

Fig. 5. The relationship between the mean Chl-*a*-specific community respiration (CR) rate of the Barents Sea community along the experiment and the average temperature treatments. The solid line shows the fitted logistic regression equation, which defines a threshold temperature (±SE) of 5.06±3.02 °C above which average specific CR rates (±SE) approximately double from a mean rate of 3.75±0.90 µmol O_2 µg Chl-*a*$^{-1}$ day^{-1} at lower temperatures to a mean rate of 7.71±0.74 µmol O_2 µg Chl-*a*$^{-1}$ day^{-1} at warmer temperatures.

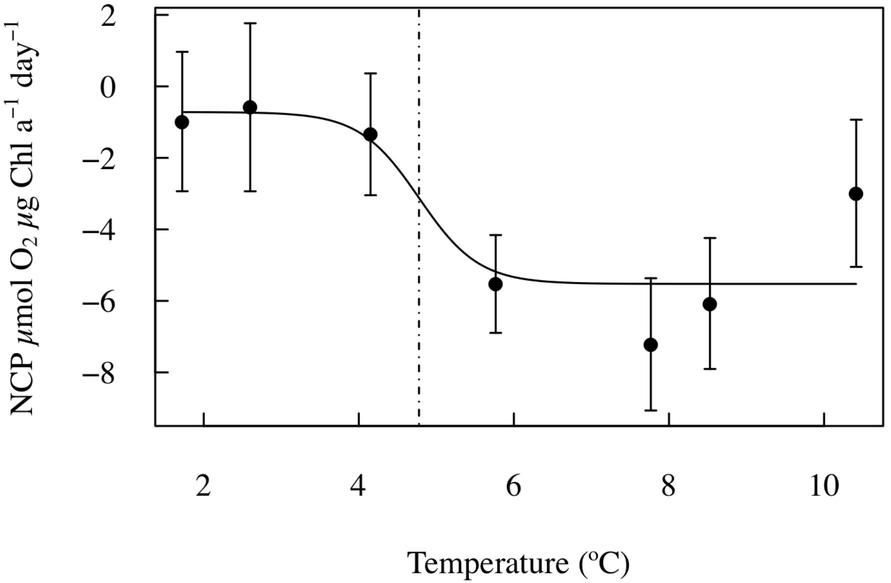

Fig. 6. The relationship between the mean net community production (NCP) rate of the Barents Sea plankton community along the experiment and average temperature treatments. The solid line shows the fitted logistic regression equation, which defines the threshold temperature (±SE) of 4.78 ± 1.26 °C above which average specific NCP rates (±SE) decrease from a mean rate of −0.72 ± 1.31 µmol O_2 µg Chl-*a*$^{-1}$ day^{-1} at lower temperature to a mean rate of −5.52 ± 1.05 µmol O_2 µg Chl-*a*$^{-1}$ day^{-1} at warmer temperatures.

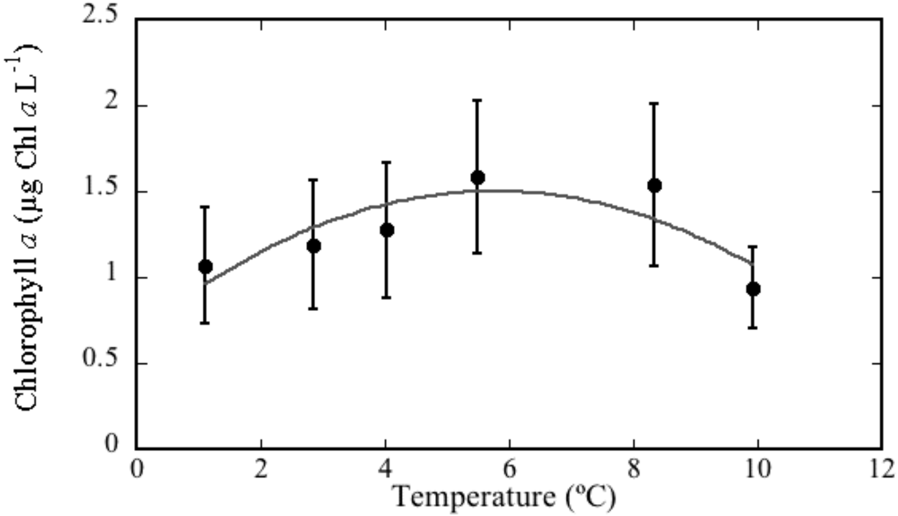

Fig. 7. Mean (±SE) chlorophyll-*a* concentration (µg Chl-*a* l^{-1}) of the Atlantic fjord community tested here, averaged over the days when samples for determination of metabolic rates were taken, versus the mean temperature (°C) recorded for each experimental treatment.