



## Mechanistic model identifies increasing light availability due to sea ice reductions as cause for increasing macroalgae cover in the Arctic

K. J. N. Scherrer,<sup>1</sup> S. Kortsch,<sup>3</sup> Ø. Varpe,<sup>2,4</sup> G. A. Weyhenmeyer,<sup>5</sup> B. Gulliksen,<sup>3</sup> R. Primicerio<sup>3</sup>

<sup>1</sup>Department of Earth Sciences, Uppsala University, Uppsala, Sweden

<sup>2</sup>Department of Arctic Biology, University Centre in Svalbard, Longyearbyen, Norway

<sup>3</sup>The Faculty of Biosciences, Fisheries and Economics, UiT The Arctic University of Norway, Tromsø, Norway

<sup>4</sup>Akvaplan-niva, Fram Centre, Tromsø, Norway

<sup>5</sup>Department for Ecology and Genetics, Limnology, Uppsala University, Uppsala, Sweden

### Abstract

In the Arctic, rising seawater temperatures and increasing underwater light caused by reductions in sea ice cover are expected to change the structure of arctic marine communities. Substantial, sometimes sudden, increases in macroalgal productivity and biomass have already been observed in arctic rocky bottom communities. These macroalgal responses have been attributed to increasing temperature and light, but the relative importance of the suggested drivers of change has not yet been assessed. In this study, we used a mechanistic competition model to unravel the effects of temperature and light on benthic community structure and algae dominance, focusing on key algae species: red calcareous algae and macroalgal fronds. We find that light is the primary driver of increases in macroalgal coverage, whereas increased seawater temperature plays a secondary role. Shifts leading to macroalgae dominated communities may be mediated by competitive interactions, and are likely due to three light-related processes: earlier sea ice break-out at high latitudes can result in an exponential increase in the cumulative amount of light that enters the water column during a year; threshold effect in light requirements for algal growth; and light requirements of calcareous algae being substantially lower than those of macroalgae. With continued warming, our modeling results suggest that reduced sea ice coverage and increased light availability will favor dominance of macroalgae, which due to their key ecological role are expected to alter the structure and functioning of arctic rocky bottom ecosystems.

The Arctic is currently warming at more than twice the average rate compared to lower latitudes (Overland et al. 2014). Rising sea surface temperatures are accompanied by rapidly decreasing sea ice cover (Comiso et al. 2008; Stroeve et al. 2011), allowing more light to enter the aquatic realm (Varpe et al. 2015). Changes in temperature and light conditions induce large alterations in species' composition and abundances in the Arctic (Wassmann et al. 2011; Fosshem et al. 2015), and are predicted to promote dominance of macroalgae in shallow benthic ecosystems (Krause-Jensen et al. 2012; Clark et al. 2013; Krause-Jensen and Duarte 2014;

Olesen et al. 2015). Supporting these predictions, 1.6 to 8-fold increases in biomass and coverage of erect macroalgae (Weslawski et al. 2010; Kortsch et al. 2012; Bartsch et al. 2016), and climate-driven increases in macroalgal growth (Marbà et al. 2017), have been documented in the Arctic during the last decades. Such changes have the potential to alter energetic pathways and reshape the habitat of other benthic organisms (Jones et al. 1994; Bruno and Bertness 2001).

In the Arctic, growth and persistence of benthic macroalgae is constrained by low water temperatures (< 5°C) and the low-light regime, as well as by mechanical ice scouring in shallow waters (Peck et al. 2009; Gómez et al. 2011; Krause-Jensen et al. 2012; Olesen et al. 2015; Bartsch et al. 2016; Marbà et al. 2017). Changing dominance patterns of macroalgae along depth transects in the Arctic (Teichert 2013) and high seaweed mortality in annually ice-covered communities (Clark et al. 2015) especially emphasize the importance of light on benthic algae composition. However, possibly because of the strong correlation between water temperature, sea ice and underwater light, the relative importance of the climatic pressures (temperature and light) suggested to be responsible for

\*Correspondence: kim.jn.scherrer@gmail.com

<sup>3</sup>Present address: Institut de Ciència i Tecnologia Ambientals, Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Spain

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the observed macroalgal increases in the Arctic has not yet been addressed.

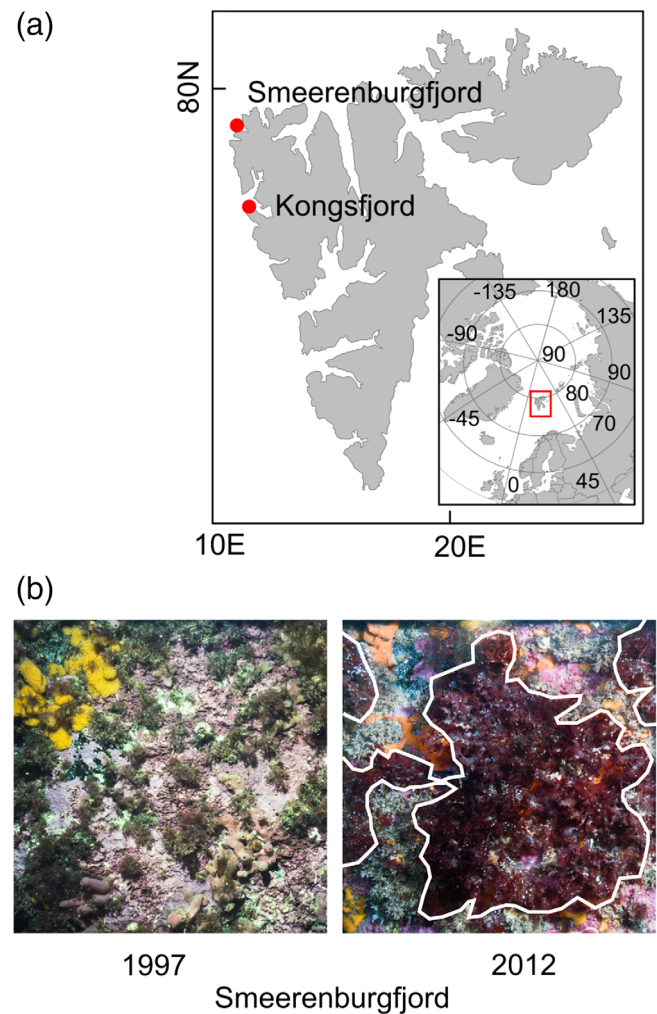
Shallow rocky bottom communities under seasonal sea ice cover in the polar regions often resemble benthos inhabiting greater depths at lower latitudes. These communities are commonly dominated by red calcareous algae, invertebrates and sessile suspension feeders (Fig. 1b; Clark et al. 2013). The importance of erect macroalgae in these arctic habitats has been found to increase nonlinearly with warming (Kortsch et al. 2012) and to increase with decreasing latitude (Krause-Jensen et al. 2012). As the ability of different macroalgae (including calcareous algae) to compete for space, via, e.g., overgrowth, antifouling mechanisms, and allelopathy, can determine dominance patterns in rocky-bottom communities (Johnson and Mann 1986; Worm and Karez 2002; Vermeij et al. 2011; McCoy and Pfister 2014), competition between calcareous algae and macroalgae may be an important mechanism influencing the transition into a macroalgal-dominated community state.

In this modeling study, we evaluated alternative causes for climate-induced macroalgal increases in arctic rocky bottom communities using a mechanistic model of algal growth that incorporates competition for space. Our aim was to examine how climate-driven changes in temperature and light, via their effects on algal growth, are likely to drive shifts in benthic macroalgal cover. Based on findings from a previous study on polar seaweeds (Clark et al. 2013), we hypothesized that increased light availability due to reduced ice coverage is a main trigger of macroalgal shifts. We focused on the dynamics of two key algae types, erect macroalgal fronds and calcareous algae, while excluding other benthic components from the model. Focusing on the dynamics of a few key species assumed to mediate higher order effects is a powerful heuristic approach to explain complex community-level responses (Godfray and May 2014). With our modeling approach, we suggest a process-based framework for understanding the mechanisms behind climate-driven macroalgal increases in polar regions.

## Materials and methods

### Modeling approach and study area

In this study, we modeled the response of subtidal arctic rocky-bottom algae communities to changes in temperature and light conditions. As a baseline for model construction, we used the observations of changes in benthic community structure from a 30-yr-long study in Svalbard, where coverage of macroalgal fronds in the shallow subtidal increased rapidly up to eight-fold (Fig. 1a,b; Beuchel et al. 2006; Beuchel and Gulliksen 2008; Kortsch et al. 2012). We parameterized the model for temperature and light conditions at 15 m depth (below depths influenced by ice-scouring) in sub-arctic fjords and coastal areas.



**Fig. 1.** Map, location of case study sites and features of the studied benthic communities. **(a)** The position of Smeerenburgfjord and Kongsfjord on the west coast of Svalbard, and the location of the Svalbard archipelago in the Arctic. **(b)** Photographs of the benthic community (at 15 m depth) from the sampling plot in Smeerenburgfjord. The photograph from 1997 is representative of the community structure before the regime shift, with dominance of red calcareous algae (*L. glaciale*) and sessile suspension feeders. After the regime shift in 2000, erect macroalgal fronds (*P. rubens* among other species) dominate the available substrate (delineated by a white line in 2012).

We modeled two key types of macroalgae involved in the documented regime shifts (Kortsch et al. 2012), and widely distributed in the Arctic: red calcareous algae (*Lithothamnion glaciale*), a group that dominates available rocky-bottom substrate (60%) in large parts of the Arctic (Johansen 1981), and erect brown and red macroalgal fronds (*Desmarestia* spp. and *Phycodrys rubens*), initially present only in low abundances (< 8% of area cover). Based on observations of space preemption and overgrowth in the Arctic (Konar and Iken 2005; Kortsch et al. 2012), and of competitively induced growth rate reductions and allelopathy from lower latitudes (Suzuki et al. 1998; Airoldi 2000; Vermeij et al. 2011), we assumed that

competition for space between calcareous algae and macroalgae takes place, and hypothesized that competition may impact the transition between calcareous algae and macroalgae dominated states. In our model, calcareous algae (C) dominance and erect macroalgal fronds (M) dominance represent the community states before and after the shifts. When referring to both benthic macroalgae types (C and M) we hereafter use the term “algae,” whereas “macroalgae” refers to the macroalgal fronds (M).

### Model formulation

We used a spatially implicit model, originally developed by Crowley et al. (2005), to investigate the dynamics of interacting calcareous algae and macroalgae. The model simulates the fraction of an arbitrary space covered by each algae type and represents appropriation of unoccupied space and overgrowth in already occupied space, mechanisms characteristic for communities of sessile organisms. The change of a species' fraction of total area cover depends on the growth rates, death rates and competitive abilities of the interacting species. The rate of change in algal area coverage was defined by the coupled ordinary differential equations:

$$\frac{dC}{dt} = g_C CA + MC(\alpha_{CM}g_C - \alpha_{MC}g_M) - d_C C \quad (1)$$

$$\frac{dM}{dt} = g_M MA + MC(\alpha_{MC}g_M - \alpha_{CM}g_C) - d_M M \quad (2)$$

where  $C$  and  $M$  are the fractions of space occupied by the two algae types,  $A$  is the fraction of unoccupied space ( $A = 1 - M - C$ ),  $g$  ( $\text{yr}^{-1}$ ) is the growth rate of the algae into unoccupied space,  $\alpha$  (dimensionless) is the contact competition coefficient, and  $d$  ( $\text{yr}^{-1}$ ) is the death rate. The reduction in growth of macroalgae when trying to establish in an area occupied by calcareous algae is given by  $\alpha_{MC}$ , whereas  $\alpha_{CM}$  is the reduction in growth of calcareous algae in areas with macroalgae. The competition coefficients  $\alpha_{CM}$  and  $\alpha_{MC}$  have values between 0 and 1, where values close to zero indicate a large reduction of the growth of the “invading” species. The net overgrowth, i.e., the “winner” in already occupied space, is determined by the difference between overgrowth rates  $g_C\alpha_{CM}$  and  $g_M\alpha_{MC}$ . Competition terms in our model represent the combined effect of several mechanisms, including overgrowth, physical antifouling, allelopathy, and any other mechanism that will result in a reduction of the growth rate of a macroalga in the presence of its competitor. Under this premise, there is empirical support for including competition between algae in our model framework (Suzuki et al. 1998; Airoldi 2000; Konar and Iken 2005; Vermeij et al. 2011; Kortsch et al. 2012). Further, algal growth rates were assumed to be temperature and light dependent, as described below.

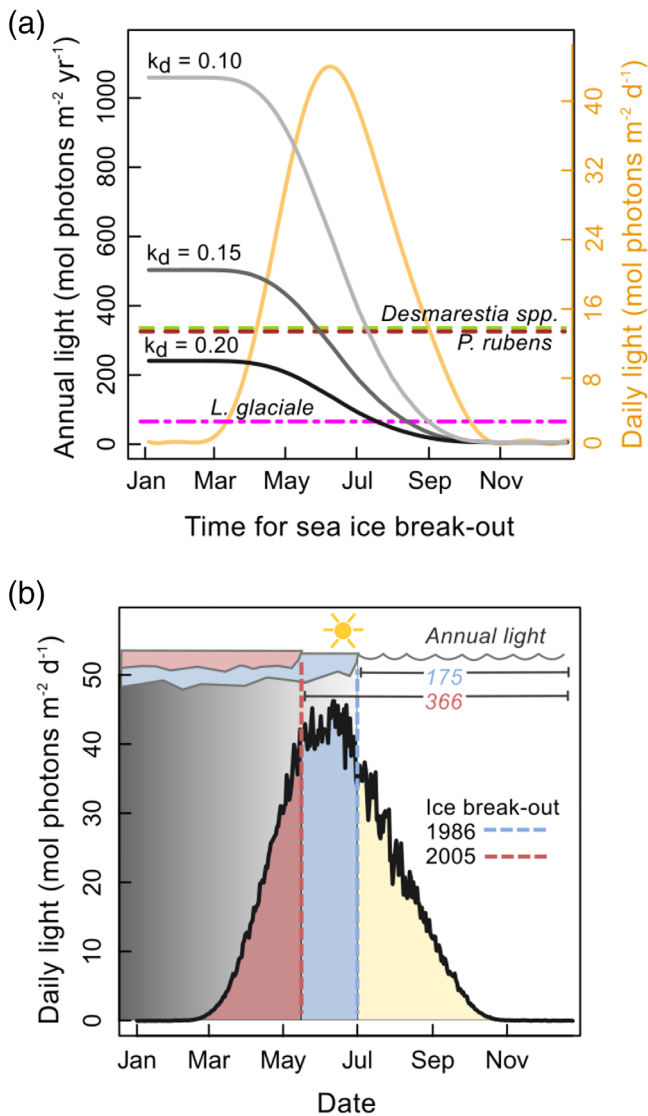
Equations 1 and 2 enable three qualitatively different final model states: (1) competitive exclusion of one species independent of initial conditions (denoted  $CxM$  or  $MxC$ ); (2) stable

coexistence between the species ( $C&M$ ); (3) start-dependent (i.e., initial cover dependent) exclusion where one species excludes the other only if it has a sufficiently high initial cover ( $C|M$ , see Crowley et al. [2005] for details).

### Annual light range in the model

We modeled light conditions at the sites, using on-land irradiance measurements from Ny-Ålesund, Kongsfjord (78.9°N, 11.9°E) performed by the Alfred Wegener Institute for Polar and Marine Research as part of the Baseline Surface Radiation Network. The average daily light for the period 1993–2015 was calculated from hourly light data corresponding to photosynthetically active radiation, converted from  $\text{W m}^{-2}$  to  $\text{mol photons m}^{-2} \text{ s}^{-1}$  by multiplying irradiance with a factor of 4.6 (McCree 1981). To model light at the sea floor we used the Beer–Lambert law for light intensity,  $I$ , at  $z$  meters depth:  $I_z = I_0 \exp(-k_d z)$ , where  $k_d$  is the light attenuation ( $\text{m}^{-1}$ ), i.e., the vertical decrease of photons in the water column. Annual light at  $z = 15$  m depth was modeled as a function of a range of possible dates for sea ice break-out and light attenuation, using the irradiance data from Ny-Ålesund as initial light intensity  $I_0$ . We summed the daily light over the ice-free days into an annual light budget (ALB). In the ALB calculations, we assumed that all days after the date for sea ice break-out were ice-free until the end of the year and that the daily contribution to the ALB was zero during ice covered days (Sakshaug et al. 2009; Clark et al. 2013). The high albedo of sea ice and snow and the strong light attenuation in snow covered sea ice (Langbehn and Varpe 2017), justify such a simplification. We omitted effects of reduced sea ice thickness, and changes in snow depth, resulting from warming for which observations are difficult to obtain, causing an underestimation of the increased light at the seafloor. Further, we did not incorporate light-reflection at the ocean surface. Modeling reflection is complex as wind and waves decrease reflectance at high latitudes (Kirk 1983), and the effect is difficult to quantify. The reduction of reflectance by wind and waves and the fact that the days with the lowest solar angle (when reflection is the highest) contribute less to the ALB motivate our assumption of no reflection. However, this assumption results in a systematic overestimation of light in our model. Based on observed light attenuation for the spring to summer period, we chose a  $k_d$  range between 0.1 and 0.2  $\text{m}^{-1}$  (Volent et al. 2007; Fricke et al. 2008; Krause-Jensen et al. 2012; Aas et al. 2013), as representative for our near-shore and relatively turbid study locations. Applying this light model to the study area produced a range of ALB at the seafloor of 100–1000  $\text{mol photons m}^{-2} \text{ yr}^{-1}$  (Fig. 2a).

We used the light model with the average daily light and an intermediate  $k_d$  of 0.15  $\text{m}^{-1}$  to estimate ALBs for two years with documented late (1 July in 1986) and early (15 May 2005) ice break-out in Kongsfjord (Svendsen 2002; Gerland and Renner 2007). We found that the ALB was



**Fig. 2.** (a) Modeled ALB at 15 m depth as a function of the date for ice break-out in the Arctic. The yellow line is a representation of daily irradiance (right y axis) which applies to Svalbard fjords. As daily light peaks around the summer solstice in late June, earlier ice melt in May–June causes a nonlinear increase in ALB. The mALB for each algae species are marked with dashed lines. The turbidity of the water, represented by the light attenuation coefficient ( $k_d = 0.10, 0.15,$  and  $0.20$ ), has a large impact on ALB. (b) ALBs at 15 m depth as a function of ice break-out date and daily irradiance exemplified for Kongsfjord, calculated for the mid-range light attenuation coefficient ( $0.15 \text{ m}^{-1}$ ). Mean daily irradiance (over the period 1993–2015) on land (black line). The dates for sea ice break-out in 1986 (blue stippled line, 01 July) and 2005 (red stippled line, 15 May). The summer solstice is indicated by the sun symbol. ALBs at 15 m depth were calculated as the sum of daily light on the seafloor on ice-free days and was more than twice as large in 2005 ( $366 \text{ mol photons m}^{-2} \text{ yr}^{-1}$ ) as in 1986 ( $175 \text{ mol photons m}^{-2} \text{ yr}^{-1}$ ).

$175 \text{ mol photons m}^{-2} \text{ yr}^{-1}$  when break-out was late and more than double ( $366 \text{ mol photons m}^{-2} \text{ yr}^{-1}$ ) when ice break-out was early (Fig. 2b).

### Temperature range in the model

Three water temperature scenarios ( $0^\circ\text{C}$ ,  $5^\circ\text{C}$ , and  $10^\circ\text{C}$ ) were used, representing averages during the algae growth season (assumed to be during summer). The scenarios capture the regularly occurring  $0$ – $5^\circ\text{C}$  surface water temperature in arctic and sub-arctic coastal areas during spring and summer (Svendsen 2002; Timmermans et al. 2017), as well as the projected  $1$ – $2^\circ\text{C}$  increase in annual average SST within the next 20 yr in the western Svalbard region (IPCC 2014). Considering that most seasonally ice-covered sites in the high Arctic are experiencing an average monthly SST in August (generally the warmest month) between  $0^\circ\text{C}$  and  $8^\circ\text{C}$  (Timmermans et al. 2017), we find the  $10^\circ\text{C}$  scenario (representing the average SST for the whole summer season) to be high but realistic. The chosen temperatures also correspond to those used as treatments in the effect studies of algae physiology underlying our parameterization.

### Model parameterization

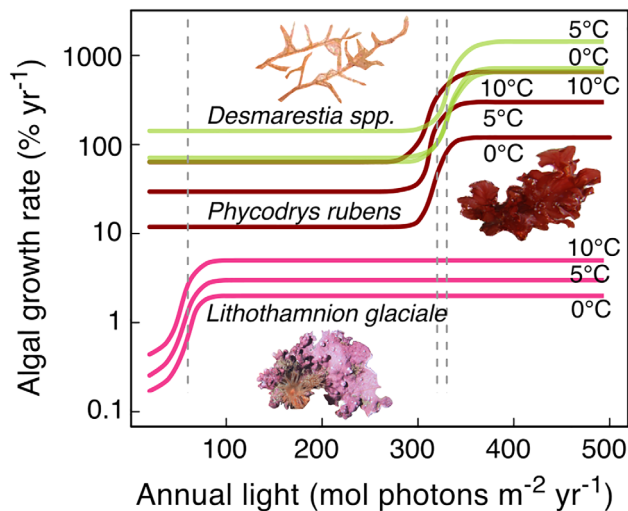
The model required estimation of three sets of parameters, i.e., growth rate ( $g$ ), death rate ( $d$ ), and contact competition coefficient ( $\alpha$ ). The growth rate for calcareous algae was obtained from Adey (1970); the yearly percent increase was calculated from the marginal growth and the average algae size, assuming a yearly growth period of 6 months (Table 1). The yearly macroalgal percent growth rates were estimated from the work by Novaczek et al. (1990) and Bischoff and Wiencke (1993) with the yearly growth period being 4 months (Schoschina 1996; Blain and Gagnon 2013). Growth rates ( $g_M$  and  $g_C$ ) were estimated for the three temperature scenarios (Table 1; Fig. 3; calculations in Supporting Information).

The death rates,  $d$ , were estimated based on the life span of the three species (Table 1); 10–50 years for the calcareous algae (Adey 1970), and 1 (*Desmarestia* spp.) or 4 (*Phycodrys rubens*) years for the macroalgae (Schoschina 1996; Blain and Gagnon 2014). The death rate,  $d$ , was determined in order to reduce an algae population from 100% to 10% in the course of the life span at zero growth rate. The yearly death rates were considered independent of temperature as the upper survival temperatures for both algae types are around  $20^\circ\text{C}$  (Adey 1970; Novaczek et al. 1990; Bischoff and Wiencke 1993), a temperature not reached in the Arctic.

As the growth rates are light dependent, we estimated the reduction in algal growth due to light limitation. We calculated the minimum ALB (mALB), i.e., the yearly light requirements of the three algae species, from their respective light compensation point,  $E_c$  (Supporting Information; Clark et al. 2013). The macroalgae had considerably higher yearly light requirements than the calcareous algae (Fig. 3; Supporting Information Tables S1 and S2). The growth rate of macroalgae not attaining its mALB was assumed to be 10% of the original growth rate without light limitation. Assuming a strong reduction in macroalgal growth rate below mALB is reasonable and in line with empirical

**Table 1.** Growth ( $g$ ), death rates ( $d$ ), and competition coefficients ( $\alpha$ ) for calcareous algae ( $C$ , *L. glaciale*) and macroalgae ( $M$ , *P. rubens* and *Desmarestia* spp.) used in the model runs for the different light, temperature, and competition scenarios. Values in parentheses indicate the growth rates used in model runs representing low-light scenarios where annual light is below the mALB of macroalgae. Temperature optimum for growth of *Desmarestia* spp. is 5°C, for the other two species approximately 10°C.

Parameter	Unit	Value			Source
		0°C	5°C	10°C	
$g_C$ lith	yr <sup>-1</sup>	0.02	0.03	0.05	Adey (1970)
$g_M$ phyc	yr <sup>-1</sup>	1.2 (0.12)	3.0 (0.30)	6.6 (0.66)	Novacek et al. (1990)
$g_M$ desm	yr <sup>-1</sup>	7.2 (0.72)	14.4 (1.44)	6.6 (0.66)	Bischoff and Wiencke (1993)
$d_C$ lith	yr <sup>-1</sup>	0.01	0.01	0.01	Adey (1970)
$d_M$ phyc	yr <sup>-1</sup>	0.5	0.5	0.5	Schoschina (1996)
$d_M$ desm	yr <sup>-1</sup>	2.2	2.2	2.2	Blain and Gagnon (2014)
		$\alpha_{CM} > \alpha_{MC}$	$\alpha_{CM} = \alpha_{MC}$	$\alpha_{CM} < \alpha_{MC}$	
$\alpha_{CM}$	—	0.9	0.5	0.2	
$\alpha_{MC}$	—	0.01	0.5	0.6	



**Fig. 3.** Summary of light and temperature effects on algal growth rates as used in model parameterization. Growth rate of *L. glaciale* (pink), *P. rubens* (brown), and *Desmarestia* spp. (green), as a function of water temperature and ALB at the seabed. mALB requirements (mol photons m<sup>-2</sup> yr<sup>-1</sup>) for the algae are marked by gray dashed lines; *L. glaciale* = 60, *P. rubens* = 320, and *Desmarestia* spp. = 330. Annual light below mALB implied a growth rate reduction by 90%. Growth rates generally increase with increasing temperature, except for *Desmarestia* spp. with growth optimum at 5°C. Note the logarithmic scale on the y axis and the large interspecific differences in growth rate.

findings, including natural experiments (Clark et al. 2013, 2015). We chose a value (10% of unlimited growth rate) that is conservative in the context of our study. Given that the modeled range of the ALB exceeded the mALB of the calcareous algae, we assumed that the growth rate of calcareous algae ( $g_C$ ) is not light limited. As the empirical data for interaction effects of light and temperature on the growth of our modeled species was insufficient, we assumed that the effects of light and temperature on algae growth are additive.

Possible ranges for the contact competition coefficient  $\alpha$ , reflecting the ability to compete for space through, e.g., overgrowth and anti-fouling mechanisms (Crowley et al. 2005), were guided by observations indicating the possibility of both macroalgae taking over space occupied by calcareous algae ( $g_M \alpha_{MC} > g_C \alpha_{CM}$ ) and vice versa (see Supporting Information; Airoldi 2000; Konar and Iken 2005). As the competition coefficients were still poorly constrained, we determined the model outcome for three scenarios; (i) calcareous algae have higher competitive ability than macroalgae (represented by  $\alpha_{CM} = 0.9$ ,  $\alpha_{MC} = 0.01$ ), (ii) equal competition coefficients ( $\alpha_{CM} = 0.5$ ,  $\alpha_{MC} = 0.5$ ), or (iii) macroalgae have higher competitive ability than calcareous algae ( $\alpha_{CM} = 0.2$ ,  $\alpha_{MC} = 0.6$ ). We addressed the uncertainty in the estimates of competition coefficients by analyzing the model over a range of relevant coefficient values (Supporting Information Fig. S2).

### Model runs and sensitivity analysis

In summary, the model was run for each macroalgae species, for all combinations of temperature (0°C, 5°C and 10°C), competition ( $\alpha_{CM} > \alpha_{MC}$ ,  $\alpha_{CM} = \alpha_{MC}$ , and  $\alpha_{CM} < \alpha_{MC}$ ), and light (i.e., without or with a light induced macroalgal growth reduction) scenarios. The strong correlation between sea ice and temperature renders high light and high temperature scenarios somewhat unlikely, but we modeled all six light and temperature combinations for comparison. The parameter values used to reflect the different scenarios are summarized in Table 1. The final equilibrium states of calcareous algal and macroalgal cover were evaluated for each parameter combination through phase-plane analysis and evaluation of numerical realizations. To investigate the effects of changing macroalgal growth rate ( $g_M$ ) and competitive ability of calcareous algae ( $\alpha_{MC}$ ) on equilibrium states we modeled the equilibrium states for different combinations of  $g_M$  and  $\alpha_{MC}$  within the ranges  $g_M = 0$ –10 yr<sup>-1</sup> for *P. rubens*,  $g_M = 0$ –15 yr<sup>-1</sup> for *Desmarestia* spp. and

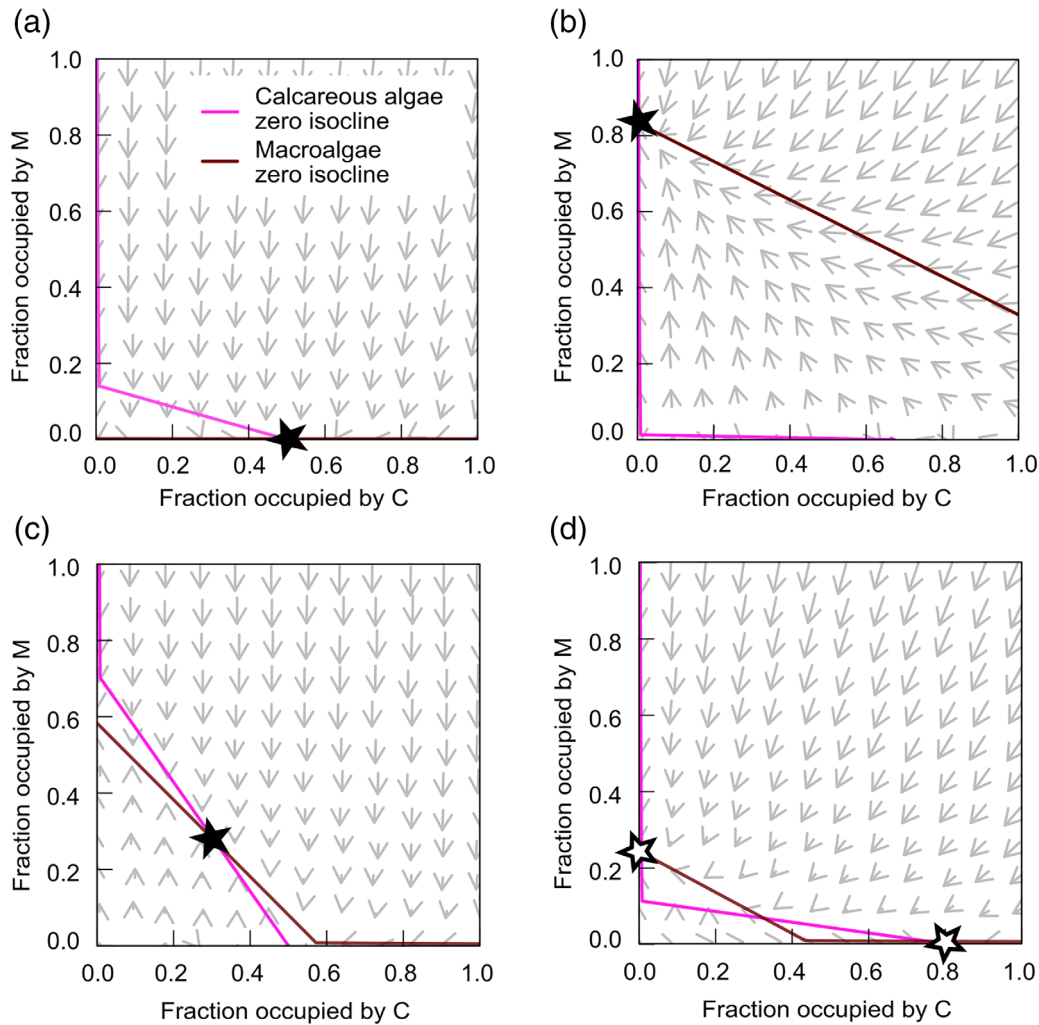
$\alpha_{MC} = 0-0.05$ . To address uncertainties in other parameter estimates, we performed a sensitivity analysis for competition ( $\alpha_{CM}$ ), mortality ( $d_C$  and  $d_M$ ) and growth ( $g_C$ ) parameters (see Supporting Information).

## Results

### Light influence on algal dominance







Under our scenarios, representing 18 combinations of temperature (0, 5 and 10°C), light (with and without light induced macroalgal growth reduction) and competition

( $\alpha_{CM} > \alpha_{MC}$ ,  $\alpha_{CM} = \alpha_{MC}$ ,  $\alpha_{CM} < \alpha_{MC}$ ), the model produced four qualitatively distinct outcomes entailing different algal dominance patterns and coexistence (Fig. 4). Model runs showed that calcareous algae outcompeted the macroalgae species if the ALB was below the mALB of the macroalgae (Fig. 4a; Table 2). Under such low annual light conditions, the calcareous algae cover ( $C$ ) stabilized between 40% and 80% of the total area, except for the 10 °C under equal competition coefficients scenario for the *P. rubens* interaction which lead to the exclusion of the species with lower initial area cover, i.e., start-dependent exclusion.



**Fig. 4.** Phase-plane diagrams illustrating the behavior of the model under different light, temperature, and competition scenarios for *L. glaciale* and *P. rubens*. The diagrams depict the vector field (gray arrows), zero isoclines for the competing calcareous algae (pink line) and macroalgae (brown line), and model equilibria (star). **(a)** When annual light is low the model generally predicts total competitive exclusion of macroalgae and a stable calcareous algae cover above 50% (here:  $g_C = 0.02$ ,  $g_M = 0.12$ ,  $\alpha_{CM} = 0.5$ ,  $\alpha_{MC} = 0.5$ ,  $d_C = 0.01$ ,  $d_M = 0.5$ ). **(b)** When macroalgae obtain their mALB calcareous algae are competitively excluded and macroalgal cover at least 60% of available substrate (here:  $g_C = 0.03$ ,  $g_M = 3$ ,  $\alpha_{CM} = 0.5$ ,  $\alpha_{MC} = 0.5$ ,  $d_C = 0.01$ ,  $d_M = 0.5$ ). **(c)** in a 0°C scenario where mALB of *P. rubens* is obtained and *L. glaciale* is a stronger competitor, the model equilibrium is stable coexistence between the species, with about 30% area coverage for both species ( $g_C = 0.02$ ,  $g_M = 1.2$ ,  $\alpha_{CM} = 0.9$ ,  $\alpha_{MC} = 0.01$ ,  $d_C = 0.01$ ,  $d_M = 0.5$ ). **(d)** in a 10°C scenario where mALB of *P. rubens* is not obtained, the outcome is dependent on initial conditions ( $g_C = 0.05$ ,  $g_M = 0.66$ ,  $\alpha_{CM} = 0.5$ ,  $\alpha_{MC} = 0.5$ ,  $d_C = 0.01$ ,  $d_M = 0.5$ ); if the initial fraction covered by *L. glaciale* is above 35% and *P. rubens* below 6% the macroalgae is outcompeted, but if the initial *P. rubens* cover is higher (above 30%) *L. glaciale* is outcompeted. The open stars represent the two possible equilibrium points, either 75% calcareous algae cover or 25% macroalgal cover.

**Table 2.** Model outcomes (algal dominance) for different scenarios involving water temperatures, competition coefficients, and light conditions (dark sun, below macroalgal mALB, yellow sun, above macroalgal mALB). Algal dominance is indicated by C, for calcareous algae, M, for macroalgae, and the subscripts p and d denoting *P. rubens* and *Desmarestia* spp., respectively. CxM (pink) refers to the outcome where calcareous algae exclude macroalgae, and MxC refers to the macroalgae *Desmarestia* spp. (green), or *P. rubens* (brown), excluding calcareous algae. C&M (gray) refers to stable coexistence between the two algae types. C|M (black) refers to start dependent exclusion.

		0°C	5°C	10°C			
$\alpha_{CM} > \alpha_{MC}$		CxM <sub>p,d</sub>		CxM <sub>p,d</sub>			
		C&M <sub>p</sub>	M <sub>d</sub> xC	M <sub>p</sub> xC	M <sub>d</sub> xC	M <sub>p</sub> xC	C M <sub>d</sub>
$\alpha_{CM} = \alpha_{MC}$		CxM <sub>p,d</sub>		CxM <sub>p,d</sub>		C M <sub>p</sub>	CxM <sub>d</sub>
		M <sub>p</sub> xC	M <sub>d</sub> xC	M <sub>p</sub> xC	M <sub>d</sub> xC	M <sub>p</sub> xC	M <sub>d</sub> xC
$\alpha_{CM} < \alpha_{MC}$		CxM <sub>p,d</sub>		CxM <sub>p,d</sub>		CxM <sub>p,d</sub>	
		M <sub>p</sub> xC	M <sub>d</sub> xC	M <sub>p</sub> xC	M <sub>d</sub> xC	M <sub>p</sub> xC	M <sub>d</sub> xC

Conversely, the macroalgae excluded the calcareous algae completely when the macroalgal mALB was obtained (Fig. 4b; Table 2) in all scenarios except when the competition coefficients favored calcareous algae ( $\alpha_{CM} > \alpha_{MC}$ ), at 0°C for *P. rubens*, and at 10°C for *Desmarestia* spp. Under such high annual light conditions, macroalgae eventually covered 60 to 90% of the surface area. The model predicted that calcareous algae could either be excluded by, or coexist with, the macroalgae (Fig. 4b,c respectively), but complete calcareous algae dominance was impossible in all nine temperature and competition scenarios under high light conditions (Table 2). At 10°C, equal competition coefficients and low light conditions, the model predicted start-dependent exclusion (Fig. 4d).

For initial conditions similar to those observed in Smeerenburgfjord before year 2000, when macroalgae covered less than 6% and calcareous algae around 45% (Kortsch et al. 2012), the model predicted that the macroalgae would go extinct. However, if initial conditions were representative of the period after year 2000 (20% macroalgae and 40% calcareous algae) the macroalgae eventually outcompeted the calcareous algae.

### Shifts in algal dominance

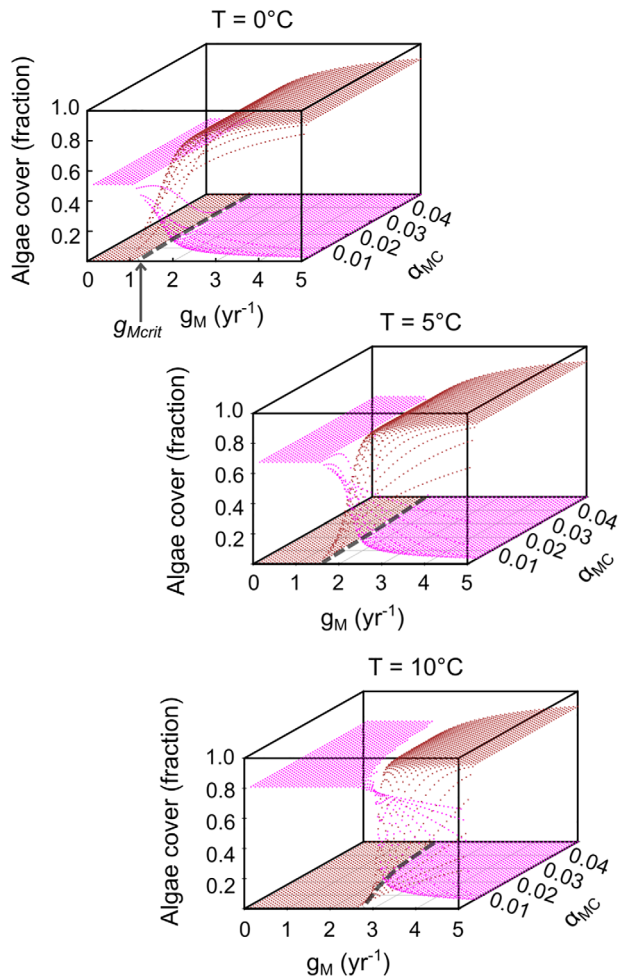
For both macroalgae species, as parameters  $g_M$  and  $\alpha_{MC}$  were gradually changed, algal dominance shifted from a state

with exclusion of macroalgae to one with exclusion of calcareous algae around a certain macroalgal growth rate, that we here denote  $g_{Mcrit}$  (Figs. 5 and 6). The critical growth rate  $g_{Mcrit}$  for a shift in dominance, counter to our expectations, increased with temperature. If the competitive ability of calcareous algae was sufficiently low (i.e.,  $g_M \alpha_{MC} > g_C \alpha_{CM}$ ), intermediate macroalgal growth rates ( $g_M$ ) enabled start-dependent exclusion, C|M (Fig. 6).

We found that the parameter space (combinations of  $g_M$  and  $\alpha_{MC}$ ) leading to start-dependent exclusion widened with temperature, with a threefold increase when going from the 0 to 10°C scenario for both macroalgae species (Fig. 6). A higher macroalgal death rate ( $d_M$ ), as well as a higher competitive ability of macroalgae (low  $\alpha_{CM}$ ), also increased the parameter space for which C|M was possible (Supporting Information Fig. S1). However, in almost all temperature scenarios, the parameterized macroalgal growth rates were above the critical threshold for their dominance if their light requirements were met (Figs. 5 and 6).

### Stable coexistence

The simulated community entered a state of stable coexistence (C&M, gray area in Fig. 6) for intermediate macroalgal growth rates and high competitive ability of calcareous algae (i.e., low  $\alpha_{MC}$ ). The parameter space enabling stable



**Fig. 5.** Equilibrium algae cover at 0°C, 5°C, and 10°C as a function of the macroalgal growth rate ( $g_M$ , x axis) and competition coefficient value ( $\alpha_{MC}$ , y axis). Competing species are *L. glaciale* (pink area) and *P. rubens* (brown area). Fixed parameter values:  $\alpha_{CM} = 0.5$ ,  $d_C = 0.01$ , and  $d_M = 0.5$ . Temperature-dependent values of  $g_C$  are 0.02 (0°C), 0.03 (5°C), and 0.05 (10°C). When  $g_M$  reaches the critical growth rate ( $g_{Mcrit}$ , between 1 and 2.5  $\text{yr}^{-1}$  depending on temperature scenario), the model equilibrium shifts from competitive exclusion of macroalgae to exclusion of calcareous algae.

coexistence broadened with increasing temperature (Fig. 6). The parameter range for which stable coexistence was possible was larger when the competitive ability of macroalgae was relatively low (i.e., high  $\alpha_{CM}$ ) (Supporting Information Fig. S2). Under coexistence, the macroalgae obtained a higher area cover, and eventually became dominant, with increasing  $g_M$ .

## Discussion

Our model clearly predicted dominance of the erect red and brown macroalgae under high light conditions, and calcareous algae dominance under low light conditions. The rapid decline in sea ice extent and earlier ice break-out experienced in the Arctic since the 1980s (Hansen et al. 2014;

Onarheim et al. 2014; Renner 2014; Laidre 2015), has likely resulted in a substantial increase in light over time, and our light calculations for Kongsfjord suggest that the change has been in the magnitude that could cause macroalgal shifts (Fig. 2b). Such an increase in annual light would affect the whole photic zone, and our results imply that earlier ice break-out would also extend the depth range of macroalgae.

The Beer–Lambert light model is, however, sensitive to the value of the attenuation coefficient (Fig. 2a), and depending on proximity to river mouths, algae blooms and hydrography,  $k_d$  can vary somewhat below and above our modeled range (Volent et al. 2007; Aas et al. 2013). Increased turbidity, driven by climate change, has been suggested to counteract the light increase from a longer ice-free period at an arctic site (Bartsch et al. 2016), and turbidity strongly affected the extent of macroalgal establishment in newly ice-free areas in Antarctica (Quartino et al. 2013). It is thus possible that the extent of macroalgal increase following a prolonged ice-free season may be limited by concurrent alterations in the optical properties of the water column. However, Krause-Jensen et al. (2012) found the length of the open-water period to be an excellent predictor of arctic kelp performance even though turbidity variations were omitted. Whereas realized  $k_d$  values may result in substantial underestimates or overestimates of annual light by our model, the assumption of no reflection is likely to cause a moderate overestimation. The latter would imply that our predicted timing of sea ice break-out needed to sustain a rapid macroalgal expansion should be adjusted to an earlier date for less turbid sites ( $k_d < 0.15 \text{ m}^{-1}$ ), and for more turbid sites ( $k_d > 0.15 \text{ m}^{-1}$ ) macroalgal expansion may not be possible due to light limitation. For predictive purposes, we would like to stress the importance of obtaining sea floor light measurements in Arctic benthic studies.

In our scenarios, higher temperature did not cause a shift in the algal dominance (Table 2). This is explained by the similar temperature affinities of both algae types, incorporated in the model via our literature-based parameterization. These similarities also explain why our model predicted increased critical growth rate for macroalgae dominance ( $g_{Mcrit}$ , Fig. 5) under warming. It is likely that many arctic macroalgae benefit from moderate warming considering their limited cold-adaptation (Gómez et al. 2011), as supported by observed increases in macroalgal growth rates in the Arctic (Marbà et al. 2017), but our model suggests that warming does not sufficiently favor macroalgal growth rates to trigger algal shifts.

Coexistence between calcareous algae and macroalgae is common in nature (Wilce 1994; Konar and Iken 2005), but was only supported by a narrow parameter space in our model. The limited scope for coexistence may partly be a result of model formulation where the algae may not share space. In nature, calcareous algae can tolerate overgrowth by macroalgae (Miles and Meslow 1990; Airoldi 2000; Dethier and Steneck 2001), enabling coexistence despite high

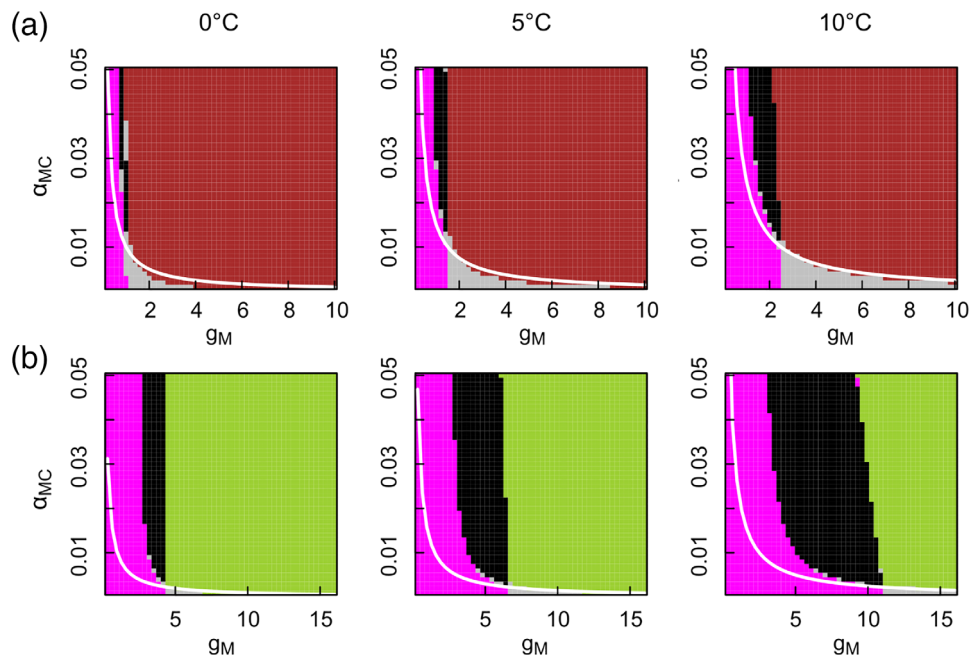


macroalgal growth rates. Further, grazing by invertebrates may also promote coexistence in nature (Paine and Vadas 1969; Mumby et al. 2006; Beuchel and Gulliksen 2008). This suggests that the complete exclusion of one or the other algae types ( $CxM$ ,  $MxC$ ) predicted by our model, may rather represent communities in which one algae type dominates the available substrate and the other is present in low abundance. By exploring the whole parameter space for competition under different temperatures, we find that the dominant algae type depends most strongly on the competitive ability of the calcareous algae ( $\alpha_{MC}$ ), and that calcareous algae are disadvantaged in warmer waters (Supporting Information Fig. S2). There are no experimental studies assessing the exact values of the competition coefficients for our modeled species (e.g., using the methods of Sorte and White 2013), which means that our findings regarding the competition outcomes remain somewhat hypothetical, yet likely under these scenarios. Our study highlights the need for controlled experiments that assess mechanisms of interactions and quantify interaction strength among species.

In seasonally ice-covered systems, earlier sea ice melt is proposed to cause light-driven macroalgae tipping points through (i) the nonlinear increase of annual light on the seafloor that accompanies a prolonged ice-free season at high latitudes and (ii) the physiological threshold effect of light on algal growth

(Clark et al. 2013). We combine these mechanisms with inter-specific competition, and the occurrence of start-dependent exclusion in our model implies that priority effects may play a role in light-driven macroalgal shifts (Crowley et al. 2005). A high initial coverage of calcareous algae could render the community somewhat resilient to macroalgal takeover, as has been documented in western Svalbard (Kortsch et al. 2012). By such an effect, competition may contribute to explain light-driven macroalgal regime shifts.

Our modeling study supports the hypothesis that climate-induced macroalgal shifts in shallow subtidal rocky-bottom communities are primarily driven by enhanced light availability at the sea floor due to sea ice loss, which greatly increases macroalgal growth rates. We find that higher water temperature plays only a secondary role for the expansion of macroalgae, even though our study covers a potential increase in summer average SST up to 10°C. A prolonged ice-free season is thus likely to be the main cause for the observed vegetation changes of arctic coasts (Weslawski et al. 2010; Kortsch et al. 2012; Krause-Jensen et al. 2012; Bartsch et al. 2016). Considering the rapid rate of sea ice retreat, further process-oriented experimental studies of polar benthic communities are urgently needed to decisively establish the mechanisms of ongoing ecological change in the Arctic.



**Fig. 6.** Qualitative model outcomes at 0°C, 5°C, and 10°C for the interaction between calcareous algae and **(a)** *P. rubens* ( $M_p$ ), and **(b)** *Desmarestia* spp. ( $M_d$ ). The pink area represents a region of competitive exclusion of macroalgae ( $CxM$ ). The brown ( $M_pxC$ ) and green ( $M_dxC$ ) areas represent competitive exclusion of calcareous algae. The gray area is a region of stable coexistence ( $C&M$ ) and the black shows start-dependent exclusion ( $C|M$ ). White lines represent the  $\alpha_{MC}$  value at which the respective overgrowth rates are equal ( $g_C\alpha_{CM} = g_M\alpha_{MC}$ ), assuming that  $\alpha_{CM} = 0.5$ . Below this line, calcareous algae can overtake space occupied by macroalgae, and vice versa above the line. As macroalgal growth rate ( $g_M$ ) increases (e.g., due to enhanced light conditions), the model outcome either passes from complete calcareous algal dominance, through a stage of start-dependent exclusion to complete macroalgal dominance, or through stable coexistence, depending on the competitive ability of calcareous algae ( $\alpha_{MC}$ ). The parameter range for which start-dependent exclusion was possible increased with temperature.

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#### Conflict of Interest

None declared.

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