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Light, temperature and competition

– understanding the causes for climate-driven regime shifts in arctic marine benthos

Kim Scherrer

ABSTRACT

Light, temperature and competition – understanding the causes for climate-driven regime shifts in arctic marine benthos

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In the Arctic, shallow sea-floor communities have been documented to shift abruptly from an invertebrate-dominated state to a state with high macroalgal abundance. Climate warming, resulting in increased water temperatures and decreased sea ice cover, could trigger such regime shifts in benthic ecosystems, but the underlying mechanisms are not clear. To gain a better understanding, a mechanistic model of algal growth and interspecific competition was applied in two marine ecosystems in northwestern Svalbard. Unravelling the effects of light and temperature on the model parameters, the current study showed that light is a key factor determining the algal dominance in the two ecosystems. Changes in sea-ice cover, which alters the underwater light regime, is therefore considered the most likely trigger for invertebrate-algae regime shifts. A continued prolonging of the ice-free season in the Arctic is likely to occur in the upcoming years, considering the current climatic development. Thus, it is expected that macroalgal cover in shallow rocky-bottom communities will continue to increase, altering species composition and function in seasonally ice-covered arctic ecosystems.

Keywords: macroalgae, light, invertebrate, coralline algae, Arctic, benthic, regime shift, climate change

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REFERAT

Ljus, temperatur och konkurrens – att förstå orsakerna till klimatdrivna regimskiften i arktiska havsbottenekosystem

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I ekosystem på grunda havsbottnar i Arktis har snabba, kraftiga förändringar i artsammansättning och ekosystemstruktur dokumenterats. Organismsamhällen som tidigare främst utgjorts av ryggradslösa organismer och hårda kalkalger har plötsligt blivit dominerade av olika tångarter. Den globala uppvärmningen medför högre ytvattentemperatur och minskat havsistäcke i Arktis, vilket i sin tur innebär förbättrade ljusförhållanden. Dessa förändringar tros kunna utlösa regimskiften där de ekosystemen övergår från ett stadium dominerat av ryggradslösa djur, till ett stadium dominerat av tång. Mekanismerna bakom sådana regimskiften är emellertid inte kartlagda. Denna studie syftade därför till en bättre förståelse för regimskiften i Arktiska havsbottenekosystem. En mekanistisk modell för algtillväxt och konkurrens tillämpades på två marina organismsamhällen i nordvästra Svalbard, som genomgått sådana regimskiften. Temperatur- och ljusberoendet hos modellens parametrar uppskattades först utifrån kunskap från ett antal tidigare studier. Med hjälp av modellen testades sedan hur fördelningen av alger påverkades av temperatur- och ljusförändringar. Modelleringen indikerade att ljusförhållanden var avgörande för expansionen av tång i de två studerade organismsamhällena på Svalbard, och att ljusförändringar således kan vara en huvudsaklig orsak till regimskiften i Arktis. Med tanke på den nuvarande klimatutvecklingen är en fortsatt förlängning av den isfria säsongen mycket sannolik. Detta kommer troligen innebära en vidare expansion av tång samt förändrad artsammansättning och ekosystemfunktion i grunda, arktiska havsbottenekosystem.

Nyckelord: marin ekologi, tång, kalkalg, Arktis, regimskifte, klimatförändring, ljus

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PREFACE

This master's thesis is made as the final, independent part of the M.Sc. in Environmental and Water Engineering at Uppsala University and corresponds to 30 ETCS. It was started in Svalbard, finalized in Stockholm, and always greatly progressed by my visits to Tromsø. During the spring semester I was an exchange student at the University Centre in Svalbard (UNIS) and apart from giving me the opportunity to work with this master's thesis, the five months in the worlds northernmost settlement was a life changing experience.

Many persons have contributed to this work. First of all I want to thank my main supervisor and co-supervisor, Raul Primicerio and Susanne Kortsch at the Nowergian College of Fishery Science, UiT the Arctic University of Norway. Without their knowledge, commitment and encouraging words this thesis could not have been made. I also want to thank my supervisor at UNIS, Öystein Varpe, Department for Arctic Biology, for his time and enlightening ideas. Thank you also to my academic supervisor at Uppsala University, Gesa Weyhenmeyer, Department of Ecology and Genetics, who has supported this thesis since the beginning.

I would like to express my thanks to the authors and publishers who have granted permission to reproduce material in this thesis. Figures 1 and 2 are reproduced by kind permission from Kortsch et al. (2012) and PNAS, figure 3 is reproduced and slightly modified by kind permission from Crowley et al. (2005) and Blackwell Publishing (© 2004 Blackwell Publishing Ltd/CNRS). Light data was kindly provided by the University Centre in Svalbard.

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POPULÄRVETENSKAPLIG SAMMANFATTNING

Ljus, temperatur och konkurrens – att förstå orsakerna till klimatdrivna regimskiften i arktiska havsbottenekosystem

Kim Scherrer

Det senaste århundradets klimatförändringar har inneburit en ökning av jordens medeltemperatur. En stor del av uppvärmningen har skett i världshavens ytvatten. Utsläpp av koldioxid, en växthusgas som har en isolerande effekt i jordens atmosfär, tros vara den huvudsakliga orsaken till temperaturökningen. Längre norrut på jorden förstärks detta fenomen, delvis på grund av ökad värmetransport mot polerna och delvis för att den istäckta ytan som reflekterar solstrålning har minskat. Medeltemperaturen i Arktis har därför stigit dubbelt så fort som det globala medelvärdet. I och med att det blivit varmare har även isförhållandena i Arktis ändrats. Utbredningen av den arktiska havsisen har minskat och den isfria perioden under sommarhalvåret har på många håll blivit längre. Ett istäcke hindrar ljus från att nå ner till havet och de organismer som lever där. Eftersom ljus och temperatur påverkar havslevande organismer, förväntas klimatförändringarna orsaka förändringar i marina, arktiska ekosystem.

På grunda, steniga havsbottnar i Arktiska kustområden finner man många olika marina växter och djur. Hårda kalkalger och olika arter av tång/sjögräs utgör grunden för ekosystemen. Dessa växter ger föda och skydd för ryggradslösa djur och fiskar. Havsanemoner, sjöborrar, svampdjur, sjöstjärnor och musslor är exempel på vanliga bottenlevande djur i arktiska ekosystem. I kustområdena kring Svalbard, en ögrupp belägen norr om den skandinaviska halvön, har forskare dokumenterat snabba, kraftiga förändringar i sådana havsbottenekosystem. Under 1980-talet dominerades havsbottnen i två fjordar på Svalbard av kalkalger och ryggradslösa djur. Men plötsligt, i mitten av 1990-talet och början av 2000-talet, skiftade ekosystemens karaktär. Olika tångarter tog över, och täcker ännu stora delar av havsbottnen. Detta så kallade regimskifte har gynnat vissa bottenlevande djurarter medan det missgynnat andra. På så sätt har hela ekosystemets struktur och egenskaper förändrats. Frågan som ställdes i den här studien är vad som orsakat denna förändring, och mer specifikt: hur kan förändringar i temperatur och ljus göra så att tångarter blir dominerande i Arktiska havsbottenekosystem?

För att förstå mekanismerna bakom ekosystemförändringarna undersöktes förhållandet mellan de två algarter som karaktäriserar ekosystemen före och efter regimskiftena i de två fjordarna. Kalkalger och tång konkurrerar om utrymmet på havsbotten. Därför skapades i denna studie en matematisk modell som beskrev tillväxten och utbredningen av kalkalger respektive tång över tid. Arternas respektive tillväxthastighet och deras konkurrenskraft gentemot varandra var de parametrar som ansågs ha störst inverkan på modellens utfall. Utfallen innebar antingen att 1) en art utkonkurrerade den andra oavsett hur stor yta de båda arterna täckte från början, 2) båda arterna samexisterade, eller 3) en art utkonkurrerade den andra enbart under förutsättningen att arten täckte ett tillräckligt stort område från början. Tidigare studier har visat att algernas tillväxthastighet är temperatur- och ljusberoende. Genom denna kunskap kunde modellutfallen bestämmas för tre temperaturscenarion och två ljusscenarion. Arternas respektive konkurrenskraft var minde väl utforskad, men utfallen för tre hypotetiska konkurrensscenarion undersöktes också.

Modelleringen indikerade att ljusförhållanden var den faktor som främst avgjorde huruvida kalkalger eller tång blev dominerande i ett arktiskt bottenekosystem. Om lite ljus årligen nådde havsbottnen (exempelvis beroende på att ett långvarigt istäcke), blev kalkalger den dominerande arten. I nästan alla fall, oavsett temperatur eller konkurrenskraft, utkonkurrerade kalkalger tången. Om ljustillgången var högre var det däremot tången som utkonkurrerade kalkalgerna i nästan alla scenarion. Tångens tillväxthastighet vid de rådande temperaturerna i Arktis är markant högre än kalkalgernas. Ljusbegränsning skulle även kunna förklara det faktum att tång, trots sin snabba tillväxthastighet, inte kunnat expandera så kraftigt tidigare. Konkurrens mellan de två arterna är troligtvis en bidragande orsak till begränsningen av tångens utbredning, men enligt modellen skulle det krävas en mycket högre konkurrenskraft hos kalkalger än hos tång för att balansera den stora skillnaden i tillväxthastighet. Regimskiften i arktiska ekosystem föreslås därför vara huvudsakligen ljusdrivna.

Ett ljusdrivet regimskifte har potentialen att vara reversibelt. På så sätt är sannolikheten stor att ekosystemen i Arktis återgår till sitt tidigare tillstånd, med dominans av ryggradslösa djur och kalkalger, om den isfria perioden återigen blir kortare. Åtgärder för minskade utsläpp av växthusgaser kan därför förväntas ha en återställande effekt på havbottenekosystemen. Men även om den globala uppvärmingen kan bromsas är det inte särskilt troligt att den kommer att vändas inom en överskådlig framtid. Regimskiften från kalkalg- till tångdominans i arktiska ekosystem är ett exempel på hur klimatförändringar påverkar naturliga ekosystem, och dagens klimatutveckling innebär att sådana regimskiften fortsatt kan förväntas ske i grunda havsbottenekosystem i Arktis såväl som i Antarktis.

GLOSSARY

Benthos	Organisms that live on or in the seabed
Calcareous algae	Crust forming red algae with calcareous deposits contained within the cell walls
Community	An assemblage of interacting populations of different species in a particular area
Foundation species	A species that is especially important for structuring a community, e.g. through creating a special habitat or environment that can sustain other species
Hysteresis	The existence of alternative stable ecosystem states under the same external conditions
Interference competition	Direct competition between individuals through e.g. overgrowth or biochemical warfare
Interspecific competition	Competition for resources (e.g. space, light, nutrients) between individuals of different species
Invertebrates	Animals without internal skeleton/spine
Macroalgae	Erect leafy or branchy seaweeds often attached to the ocean floor (three main groups; brown algae, red algae and green algae)
Regime shift	Sudden, substantial and persistent shifts in ecosystem structure and characteristics from one state to another, alternative state
Resilience	An ecosystems capacity to resist and recover from disturbances and thus remain in its stable state
Stable state	A certain structure and character of an ecosystem which prevails under a specific range of external conditions (e.g. temperature, light, nutrient levels)
Sessile	Permanently attached or fixed to the bottom, a common feature of organisms in rocky-bottom communities
Tipping point	The point at which a regime shift occurs and the ecosystem qualitatively changes

TABLE OF CONTENTS

1 INTRODUCTION

In the Arctic, the temperature increase induced by climate warming is consistently predicted to be greater than the global average (IPCC, 2014). The temperature increase registered during the past 30-35 years (ACIA, 2004; Comiso, 2003) has been accompanied by rapidly decreasing sea-ice cover (Stroeve et al., 2007; Comiso et al., 2008), affecting the underwater light conditions (Clark et al., 2013). Wassmann et al. (2011) linked alterations in the abundances and distributions of arctic marine species to light and temperature changes which, through effects on organism physiology, impact both demography (i.e. growth, mortality, reproduction) and ecological interactions (e.g. competition, grazing, predation) (Doney et al., 2012). In particular, a prolonged ice-free season and higher sea surface temperatures (SST) promote primary production, resulting in increased macroalgal cover in shallow (0-30 m depth) rocky-bottom communities in polar regions (Clark et al., 2015; Kortsch et al., 2012; Quartino et al., 2013; Weslawski et al., 2010). Although there are many recent observations of changes in the distributions and abundances of species in the Arctic, a theoretical framework that may explain the mechanisms behind them is missing.

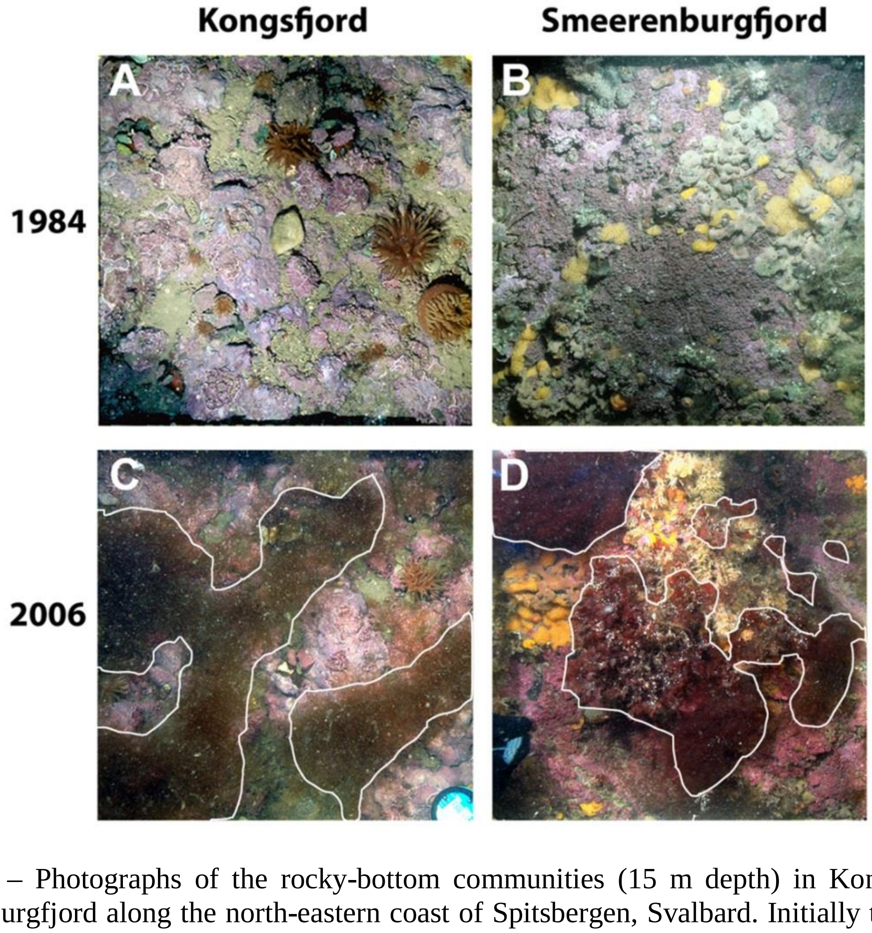

Figure 1 – Photographs of the rocky-bottom communities (15 m depth) in Kongsfjord and Smeerenburgfjord along the north-eastern coast of Spitsbergen, Svalbard. Initially the sea floor communities were dominated by pink coloured crustose coralline algae (of family Corallinaceae) and invertebrate organisms such as sponges, sea anemones, barnacles and sea squirts. After the observed shifts, erect red and brown macroalgae (earlier covering less than 8 % of space), covered large areas (25-80 %) of the sea floor. The macroalgae cover is encircled with a white line. Image: Kortsch et al. (2012)/PNAS.

Box 1 - What is a rocky-bottom community?

Shallow rocky-bottom communities are highly productive and diverse ecosystems, sustaining important ecosystem functions such as nutrient cycling, primary production and water purification. They are characterized by a hard bottom surface made up by rocks or boulders and little sedimentation, allowing sessile organisms (organisms permanently attached to a substrate) to attach and grow. Light, which attenuates rapidly in water, still reaches down to the shallow sea floor and the zone is affected by water movements, run-off from land and temperature changes to a greater extent than deep sea bottoms.

In the Arctic, rocky-bottom communities are generally inhabited by invertebrates (i.e. animals without internal skeleton) such as sponges, moss animals (bryozoans), mussels, sea squirts (ascidians), grazing sea urchins and predators such as sea anemones and starfish (Gulliksen and Svensen, 2004). Many of these bottom living, or *benthic* animals, are sessile. This also applies to benthic algae. The pink colored crustose coralline algae, rock-like algae with a hard calcareous skeleton, are abundant in the Arctic, but large brown, red or green macroalgae with a three-dimensional structure are also widely distributed (Figure 1).

Competition for space is a key structuring force in rocky-bottom communities (Sommer and Worm, 2002); sessile organisms need free substrate to attach to and grow (Paine, 1984) and in the absence of large perturbations, new space is mainly freed when organisms die (Dayton et al., 1974; Witman and Grange, 1998). This gives rise to a variety of competition mechanisms including overgrowth (Quinn, 1982; Sebens, 1986), physical anti-fouling mechanisms (Johnson and Mann, 1986) and biochemical warfare (Da Gama et al., 2014). Organisms also compete indirectly when they have to share limiting resources such as light and nutrients. Such interspecific interactions may cause non-linear dynamics in ecosystems (Molis and Gama, 2009) and the temperature dependence of the competitive ability of species is thought to be an important factor for shifts in species dominance (Sorte and White, 2013).

Shifts in algal dominance have consequences for the structure and functioning of the whole seabed (i.e. benthic) ecosystem. Macroalgae are considered foundation species and ecosystem engineers (Bruno and Bertness, 2001; Jones et al., 1994), i.e. they provide both food and habitat for other species (Blain and Gagnon, 2014). In a study by Kortsch et al. (2012), the rocky-bottom communities in two arctic fjords were monitored during 1980-2010. At both sites, Kongsfjord and Smeerenburgfjord situated on the northwest coast of Svalbard (Figure 2A), substantial and abrupt reorganizations of the rocky-bottom communities, involving rapid macroalgal expansion, were observed (Figure 1). The authors proposed that reduced sea ice and increased sea-water temperatures were involved in promoting a new ecosystem state. In a similar polar environment, Clark et al. (2013) studied the effect of changing sea-ice conditions on coastal benthic communities in Antarctica, concluding that only a slight sea-ice decline (i.e. increase in annual light) may cause shifts from an invertebrate-dominated to a macroalgae-dominated state.

The above large, abrupt and rapid shifts in community structure caused by linear changes in environmental drivers can be referred to as regime shifts (Carpenter, 2003; Scheffer et al., 2001). Most observed regime shifts in marine ecosystems have been recorded at lower latitudes, e.g. algal expansion in coral reefs (Bellwood et al., 2004) and shifts in species abundance and composition in the North Sea (deYoung et al., 2004). Observations of regime shifts in the Arctic are rare, most likely because few long-term studies have been conducted (Wassmann et al., 2011). However, regime shifts have been detected in lake ecosystems (Smol et al., 2005) and in sub-arctic rocky-bottom communities (Kortsch et al., 2012)

The main goal in this study was to find out whether 1) temperature, 2) light, or 3) interspecific competition could explain the rapid shift from invertebrate- to macroalgae-dominated state in arctic rocky-bottom communities. The regime shifts observed in Kongsfjord and Smeerenburgfjord (Kortsch et al., 2012) provided the theoretical basis and worked as case study systems. Three competing algae types, *Lithothamnion glaciale*, *Desmarestia spp.* and *Phycodrys Rubens*, were chosen to represent the ecosystem states before and after the regime shifts. These algae species were involved in the reorganization of the benthic communities in northwestern Svalbard. A mechanistic model of algal growth, originally developed by Crowley et al. (2005), was used to investigate the dynamics of the interacting algae species. It was assumed that light and temperature changes are the main drivers of change in arctic rocky-bottom communities. Thus, the effects of these climatic drivers on the algal growth rates were estimated from earlier studies. The model, parameterized for the benthic ecosystems in Kongsfjord and Smeerenburgfjord, was used to gain a better understanding of the mechanisms underlying the documented regime shifts.

2 METHODS

Two documented regime shifts in arctic marine benthos (Kortsch et al., 2012) were used as a framework for the model construction in this study. A two-dimensional model of algal growth (developed by Crowley et al. (2005)) that simulated the relative area coverage of each algae species, was used to investigate the regime shifts. This section first summarizes the regime shifts in the case study systems and describes how the observations have been used in this modelling study. A detailed description of the algal growth model, as well as the parameter estimation, is then provided. Also, the assessment of light conditions in the case study systems, in relation to sea-ice cover, is shown.

2.1 CASE STUDY: BENTHIC REGIME SHIFTS IN NORTH WESTERN SVALBARD

The regime shifts in marine benthos in Kongsfjord and Smeerenburgfjord, Svalbard (Kortsch et al., 2012) were used as case studies, providing a basis for both the conceptual approach and model parameterization in this study. The regime shift in Kongsfjord occurred during 1995-1996 and meant that the previous community, dominated by red calcareous algae and sea anemones, was replaced by one where brown algae abundance fluctuated between very high (up to 80 %) and low (down to 8 %) area coverage (Figure 1A and 1C). In Smeerenburgfjord, the shift took place in 2000; the earlier community characterized by different sessile suspension feeders and red calcareous algae changed into one dominated by various species of erect red and brown macroalgae and bryozoans (Figure 1B and 1D).

The study by Kortsch et al., 2012 was based on a 30-year photographic survey. Photographs of the same sea-floor transects (Figure 1) were taken in August annually between 1980 and 2010, and percentage area cover of different species was determined through digital image analysis. During the same time period, the average sea surface temperature (SST) and the length of the ice-free season in the north-western Svalbard area gradually increased with 0.5 °C and 3.3 days per year (Figure 2B and 2C; Kortsch et al., 2012), the latter implying changes in light conditions on the sea-floor (Clark et al., 2013). Conditions in the fjords, situated on the north-western part of Spitsbergen in the Svalbard archipelago (Figure 2A), are influenced by relatively warm ($T > 3$ °C) and saline atlantic water, cold arctic water and fresh water from glacial melt (Cottier et al., 2005). Environmental conditions in the benthic communities are thus influenced by large-scale climate variations as well as local wind patterns, fjord morphometry and run-off (Svendsen et al., 2002). Both study sites are rocky-bottom areas at approximately 15 m depth, with the Kongsfjord site being a horizontal bottom and the Smeerenburgfjord site a vertical wall.

2.2 CONCEPTUAL APPROACH

The complex structures of Arctic rocky-bottom ecosystems have in this study been distilled down to a simplified conceptual framework. Out of the variety of organisms in the arctic rocky-bottom communities, the calcareous red algae *Lithothamnion glaciale* and its macroalgae competitors *Desmarestia spp. (D. aculeata* and *D. viridis,* brown algae) and *Phycodrys ruben*s (red algae) were chosen for this model study. A manipulation experiment in Smeerenburgfjord, where a bottom area was cleared of all organisms and the subsequent recolonization was monitored, indicated competition between these algae species (Kortsch et al., 2012). This, together with the algae’s roles as ecosystem engineers and foundation species, made them especially suitable to represent the community states before and after the shifts as well as to illustrate the regime shift itself.

Since both sea surface temperature (SST) and the length of the ice-free period have increased in the North-Western Svalbard area (Kortsch et al., 2012), the effects of light and temperature on calcareous algae and macroalgae were investigated in this study. It was hypothesized that, due to the limited cold-adaptation exhibited in arctic compared to antarctic species (Gómez et al., 2009), increasing temperature would enhance algal growth rate. Light is crucial for marine primary producers and the length of the ice-free period has been pointed out as a key predictor for biomass production and spatial distribution of macroalgae (Krause-Jensen et al., 2012). Light and temperature were thus considered external drivers, affecting growth of the investigated algae species and the interaction strength between them.

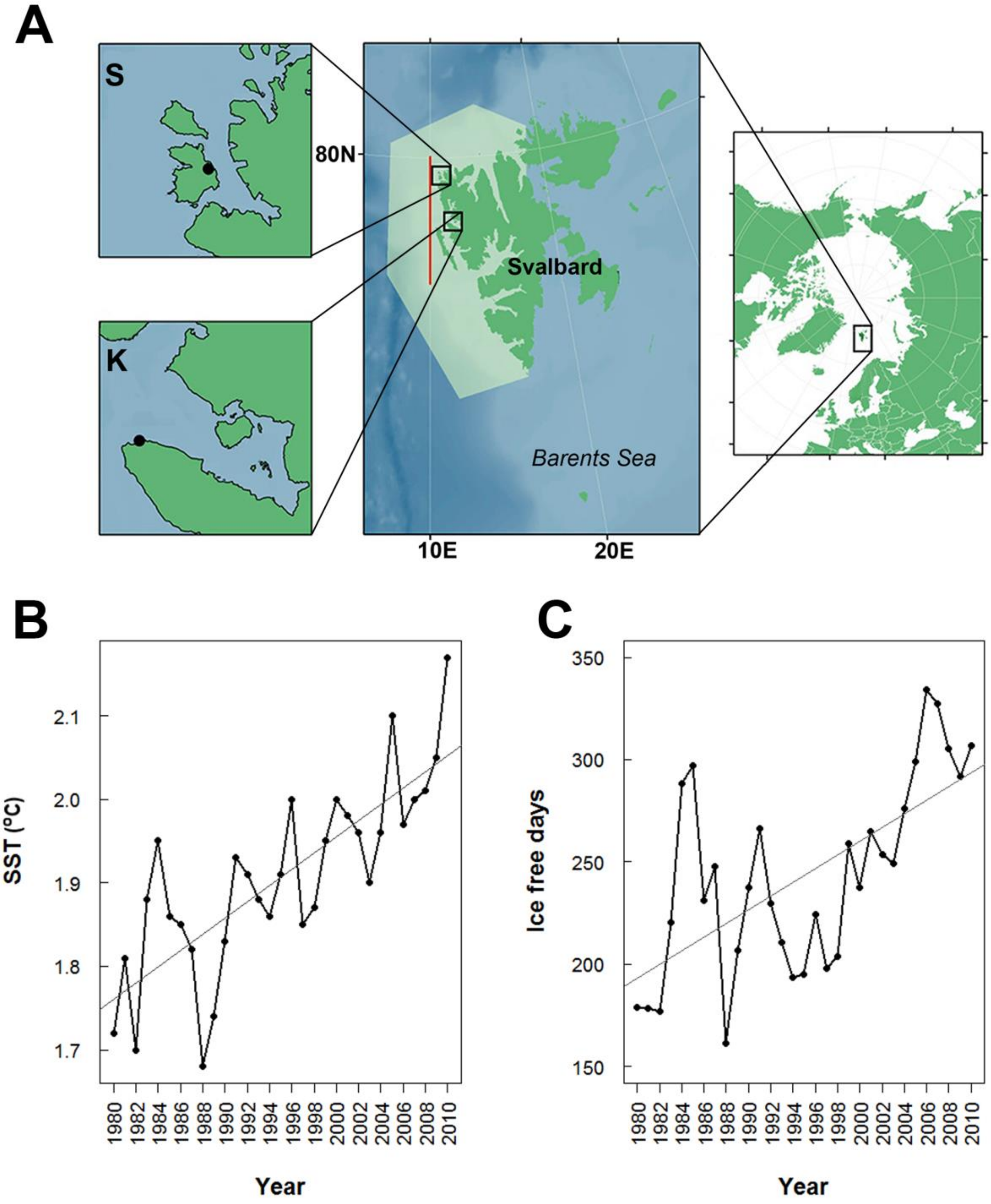

Figure 2 - Map of the case study area and time series of the sea surface temperature (SST) and length of the ice-free period. A) The location of the two study sites Kongsfjord (K) and Smeerenburgfjord (S), the position of the fjords along the coast of Spitsbergen, and the location of Svalbard in the Arctic. B) Time series of SST along the northwest coast of Svalbard (1980-2010) with linear regression (grey line) showing a yearly SST increase by 0.1 °C yr^{-1}. C) Time series of the number of ice-free days each year (1980-2010) with regression (grey line) indicating a yearly increase in the length of the ice-free season by 3.3 days yr^{-1}. Image: Kortsch et al. (2012)/PNAS.

2.3 MODEL DESCRIPTION

A spatially implicit model, originally developed by Crowley et al. (2005), was used to investigate the dynamics between the calcareous algae *Lithothamnion glaciale* and the macroalgae *Phycodrys rubens* or *Desmarestia spp.*. The model is suitable for describing competition for space between sessile organisms (Crowley et al., 2005) and it determines the areal expansion of a species dependent on its growth rate, death rate and its competitive ability. The change in area coverage is calculated by two coupled ordinary differential equations (ODEs);

$$\frac{dC}{dt} = g_C CA + MC(k_{CM} g_C - k_{MC} g_M) - d_C C \qquad \text{eq. 1}$$

$$\frac{dM}{dt} = g_M MA + MC(k_{MC} g_M - k_{CM} g_C) - d_M M \qquad \text{eq. 2}$$

where *C* and *M* are the fractions of space occupied by macroalgae and calcareous algae respectively, *A* is the fraction of unoccupied space (A=1-M-C), *g* is the growth rate of the algae species, *k* is the competition coefficient and *d* is the species specific death rate. k_{CM}, which lies between 0 and 1, tells us how much the growth of calcareous algae is reduced when in contact with macroalgae (and vice versa for k_{MC}). The first term in equation 1 represents the per-capita growth of calcareous algae into unoccupied space, while the second term describes growth of calcareous algae when in contact with macroalgae. The relation between $k_{CM}g_C$ and $k_{MC}g_M$ decides the sign of this competition term; if $k_{CM}g_C>k_{MC}g_M$ calcareous algae overgrow the macroalgae, if $k_{CM}g_C<k_{MC}g_M$ calcareous algae are overgrown by macroalgae. The last term is the per-capita death rate.

This pair of ordinary differential equations was used to test the impact of light and temperature on the relative dominance of the algae species. Model parameter estimation is described in section 2.4. The model formulation can produce four different outcomes for a certain parameter (*g*, *k* and *d*) setting;

a) competitive exclusion of *M*, over time meaning total dominance of calcareous algae over macroalgae
b) competitive exclusion of *C*, over time meaning total dominance of macroalgae
c) stable coexistence between *C* and *M* at a certain combination of equilibrium area coverage
d) start-dependent exclusion of *C* or *M*, where the initial coverage decides which species will dominate and which will go extinct

The four outcomes (Figure 3) provided the basis for a qualitative evaluation of the importance of light, temperature and interspecific competition on the benthic community structure. The model was implemented in `R` and the ODEs were solved with the function `lsoda` from the `deSolve` package, version 1.12 (Soetaert et al. 2010).

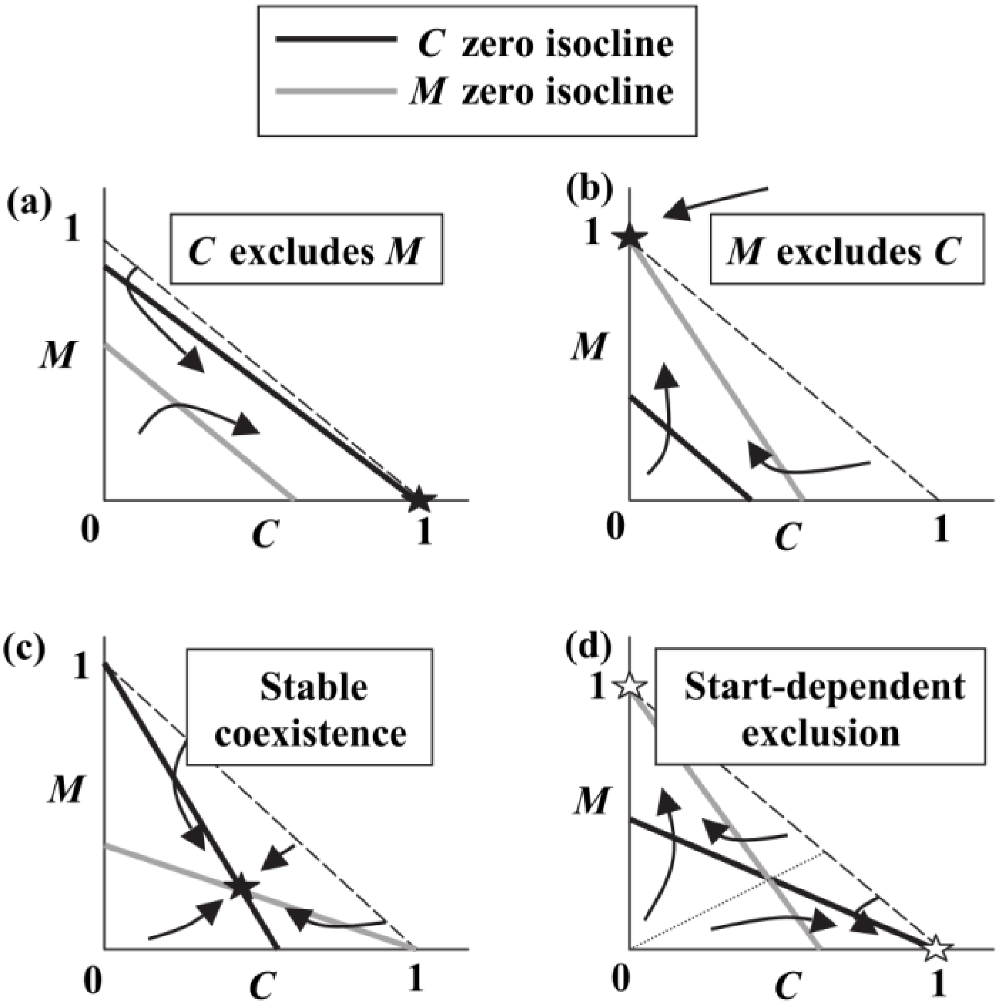

Figure 3 – Diagrams describing the four possible outcomes from the model formulation. The fraction of space that is occupied by calcareous algae (*C*), on the x-axis, is shown in relation to the fraction occupied by macroalgae (*M*), on the y-axis. For a certain time, the model predicts a certain algae distribution, e.g. 50 % calcareous algae cover and 20 % macroalgae cover, corresponding to the point (0.5, 0.2) in the diagram. We call this distribution of C and M the *state* of the ecosystem. These so-called phase plane plots summarize the model behaviour and outcome for a fixed set of parameter values through showing how the system changes from an arbitrary initial state. Arrows show the trajectories along which the state changes with time and stars mark the final equilibrium state at which the system is stable. The grey and black lines are the parameter value dependent zero isoclines, showing the states at which the coverage of a species neither grows nor decreases. When the C-isocline lies completely above the M-isocline, as in a), the model outcome will be complete exclusion of macroalgae (the opposite illustrated in b)). When the isoclines cross, the model outcome is either c) stable coexistence or d) start-dependent exclusion. Presuming, only hypothetically, that calcareous algae are better overgrowth competitors ($k_{CM}g_C > k_{MC}g_M$), stable coexistence between C and M will occur if the C-isocline intercepts the M-axis above the M-isocline, but below the M-isocline on the C-axis as in c). If the opposite isocline relation is true as in d), the initial conditions will determine which algae that will be excluded. The two domains of attraction are in d) separated by the thin dotted line. Note that under the assumption that M+C > 1, states above the dashed line are impossible. The figure was modified with permission from Crowley et al. (2005), © 2004 Blackwell Publishing Ltd/CNRS.

2.4 MODEL PARAMETER ESTIMATION

2.4.1 Growth rates, competition coefficients and death rates

Growth rate values (g_M and g_C) were estimated for three different water temperatures; 0, 5 and 10°C (Table 1). The growth rate for *L. glaciale* was obtained from Adey (1970); the yearly increase in percent was calculated from the marginal growth and the average algae size. The yearly growth rates in percent for *P. rubens* and *Desmarestia spp.* were estimated from the work by Novaczek et al. (1990) and Bischoff and Wiencke (1993) respectively. Details about the growth rate estimations can be found in Appendix A1. Due to large uncertainties concerning the competitive interactions between the calcareous algae and macroalgae, the competition coefficients k_{CM} and k_{MC} were constrained to lie between 0 and 1.

The yearly death rates were considered not to be temperature dependent since the upper survival temperatures for all three species lie around 20 °C (Adey, 1970; Bischoff and Wiencke, 1993; Novaczek et al., 1990), which is not reached in the cold study area. Thus, d was estimated based on the life span of the three species; *L. glaciale* = 10-50 years (Adey, 1970), *P rubens* = 4 years (Schoschina, 1996), *Desm spp.* = 1 year. Using the model formulation, d was determined as the death rate needed to reduce an algae population from 100 to 10 % in the course of the life span when $g = 0$; d_C *lith* = 0.01 yr^{-1}, d_M *phyc* = 0.5 yr^{-1}, d_M *desm* = 2.2 yr^{-1}.

Table 1 - Temperature dependent growth rates (g) and fixed death rates (d) for *L. glaciale*, *P. rubens* and *Desmarestia spp.*. Growth optimum for *Desmarestia spp.* is at 5 °C, for the other two species around or above 10°C.

Param	**Unit**	**Value**			**Source**
		Temp. (°C)			
		0	***5***	***10***	
g_C *lith*	yr^{-1}	0.02	0.03	0.05	Adey, 1970
g_M *phyc*	yr^{-1}	1.2	3.0	6.6	Novaczek et al., 1990
g_M *desm*	yr^{-1}	7.2	14.4	6.6	Bischoff and Wiencke, 1993
d_C *lith*	yr^{-1}	0.01			Adey, 1970
d_M *phyc*	yr^{-1}	0.5			Schoschina, 1996
d_M *desm*	yr^{-1}	2.2			

2.4.2 Effect of light on algal growth rates

To determine the reduction in algal growth due to light limitation, the yearly light requirements of the three algae species were estimated from their respective light compensation point, E_c (details in Appendix A3). E_c (µmol photons $\text{m}^{-2}\ \text{s}^{-1}$) is the irradiance level at which photosynthesis rate equals respiration rate, and can thus be considered a minimum light requirement for growth. In accordance with the work by Clark et al. (2013), E_c was used to calculate a minimal annual light budget (mALB) for each species by summing the minimum light requirement (E_c) over the year (Table 2). *Desmarestia. spp* (Johansson and Snoeijs, 2002; Kühl et al., 2001) and *P. rubens* (Johansson and Snoeijs, 2002; King and Schramm, 1976) had considerably higher yearly light requirements than *L. glaciale* (Adey, 1970; Burdett et al., 2012) (Table 2). There was however some variation between the different E_c-values stated in the literature and therefore the mean value was used.

Table 2 - Minimum annual light budget (mALB) for *Desmarestia spp., L. glaciale* and *P. rubens*, determined from E_c stated in earlier studies

Species	**mALB (mol phot. m^{-2} yr^{-1})**	**Sources**
Desmarestia spp	330	Johansson and Snoeijs, 2002; Kühl et al., 2001
Phycodrys rubens	320	Johansson and Snoeijs, 2002; King and Schramm, 1976
Lithothamnion glaciale	60	Adey, 1970; Burdett et al., 2012

Guided by the fact that growth was still recorded for light levels below the E_c of another polar seaweed, *Parmaria decipiens*, in the experiment by Clark et al. (2013), the growth rate of algae not obtaining their mALB was estimated to be 10 % of the original growth rate without light limitation.

2.5 UNDERWATER LIGHT CONDITIONS

Although the length of the ice-free period in the case study area has been determined (Kortsch et al., 2012; Figure 2), the light conditions at the investigated sites are not known. To determine a plausible light range for Kongsfjord and Smeerenburgfjord, the amount of light that reach the benthic communities was estimated from PAR (Photosynthetically active radiation) irradiance data collected in 2007 at Rijpfjorden weather station on Nordaustlandet, Svalbard (data source: the University Centre in Svalbard). An annual light budget for 15 m depth was modelled using the Beer-Lambert law for light attenuation (Appendix A2), which determines the light intensity as a function of depth. To use the Beer-Lambert law, the light attenuation coefficient (k_d), describing the transparency of the medium, had to be estimated. Close to Ny Ålesund, further in in Kongsfjorden, Fricke et al. (2008) and Volent et al. (2007) measured the average k_d for PAR in spring/summer to be approximately 0.27 m^{-1}. However, in the open waters around Svalbard, k_d has been estimated to 0.12 m^{-1} (Aas et al., 2013). The contribution to the annual light budget was considered to be negligible under ice covered conditions (Sakshaug et al., 2009) as well as during the winter months (late October to January). The annual light was determined as a function of the hypothetical time for sea-ice break-out and calculated for k_d = 0.10, 0.15, 0.20 and 0.30 (Figure 4).

The contribution to the annual light budget in Rijpfjorden at 15 m depth was largest around the summer solstice in mid-June, thus being a critical time for the light regime in benthic communities in Svalbard (Figure 4). The annual light budget was not notably affected if sea-ice beak-out occurred in February instead of April, but break-out in May instead of June increased the light budget with up to about 250 mol photons m^{-2} yr^{-1}. Light intensity on the sea floor was however greatly dependent on the light attenuation coefficient, k_d. Annual light on the sea-floor ranged from around 50 (lower than or equal to the mALB of all three algae species) if k_d was 0.30, to 1150 mol photons m^{-2} yr^{-1} (three times the mALB of the two macroalgae species) when k_d was 0.10 (Figure 4). For the macroalgae, k_d-values around 0.15-0.20 were critical for deciding if their mALB would be obtained or not (Figure 4, blue and red lines).

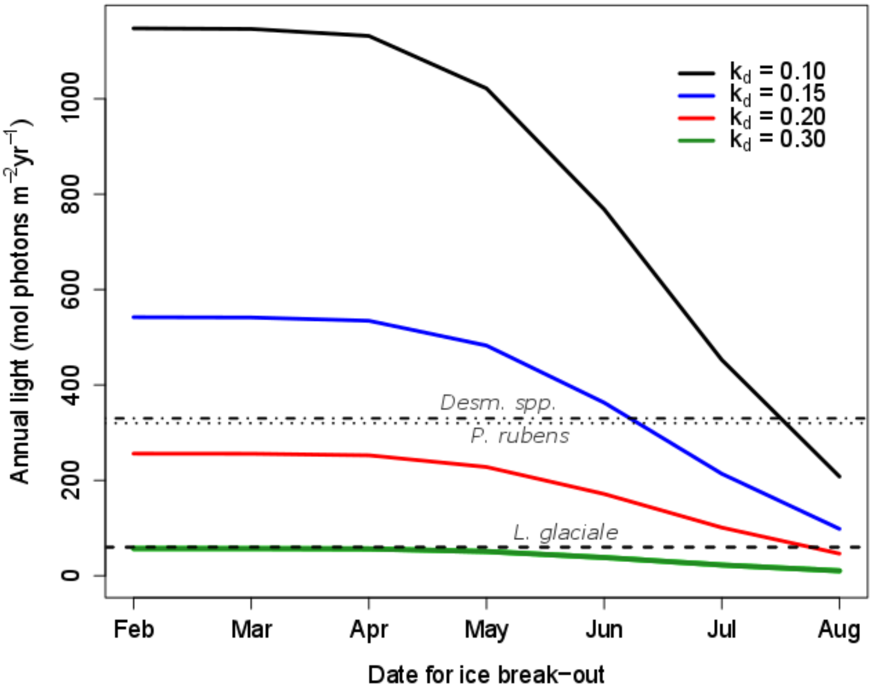

Figure 4 - The modelled annual light budget (mol photons m^{-2} yr^{-1}) at 15 meters depth in Rijpfjorden 2007, as a function of the time for sea-ice break-out and for different values on the light attenuation coefficient k_d. Incoming solar radiation is highest around the summer solstice, resulting in a non-linear decrease in annual light budget if sea-ice melt occurs in summer (e.g. mid-June) instead of in spring (e.g early May). However, the effect on the annual light is small if ice break-out normally occurs in early spring and occurs in e.g. March instead of April. The minimum annual light budget (mALB) required by each algae species are marked in the figure (*Desmarestia spp.* = dashdotted line, *P. rubens* = dotted line and L. glaciale = *dashed line*). If the mALB line is below the annual light budget, algal growth rate is significantly reduced (90 % reduction in this study). The great importance of the light attenuation coefficient, k_d, is illustrated by the four scenarios (k_d = 0.10, 0.15, 0.20 and 0.30), showing that for intermediate values (k_d = 0.15-0.20), the annual light budget can be critical for macroalgal growth.

2.6 MODELLING STRATEGY

The model (eq. 1 and 2) was used to determine how the distribution of calcareous algae (*L. glaciale*) and macroalgae (*Desmarestia spp.* or *P. rubens*) was dependent on light conditions, temperature conditions and interspecific competition. As a first step, two distinct light scenarios, obtained or not obtained mALB, were used to represent the effect of light on algal growth. It was assumed that light conditions at the case study sites were always favourable for L. glaciale, but that the macroalgae suffered a 90 % reduction in g_M when light conditions were poor, e.g. due to a short ice-free season (see section 2.5). As a first step three temperature scenarios were modelled; 0, 5 and 10 °C. Finally, three scenarios for competition were used, assuming either that calcareous algae were better ($k_{CM} > k_{MC}$), equal ($k_{CM} = k_{MC}$) or poorer ($k_{CM} < k_{MC}$) competitors for space than macroalgae. Algal cover over time was simulated and outcomes (exclusion, coexistence or start-dependent exclusion) for all light, temperature and competition scenarios were determined.

3 RESULTS

3.1 LIGHT EFFECTS

The model outcome was mainly dependent on whether the macroalgae obtained their mALB or not. Most commonly, simulations resulted in total competitive exclusion of one of the two algae species. Assuming that the annual light was higher than 60 but lower than 320 mol photons m^{-2} yr^{-1}, *L. glaciale* typically outcompeted both *Desmarestia spp.* and *P. rubens* regardless of initial algae cover distribution, temperature and competition coefficient values (Figure 7 and Figure 8), stabilizing around 40-80 % area coverage. Conversely, when the macroalgal light requirements were met, the general result was total exclusion of calcareous algae by both *P. rubens* and *Desmarestia spp.* respectively (Figure 9 andFigure 10) with *Desmarestia spp.* covering 70-85 % of the surface area and *P. rubens* 60-90 %.

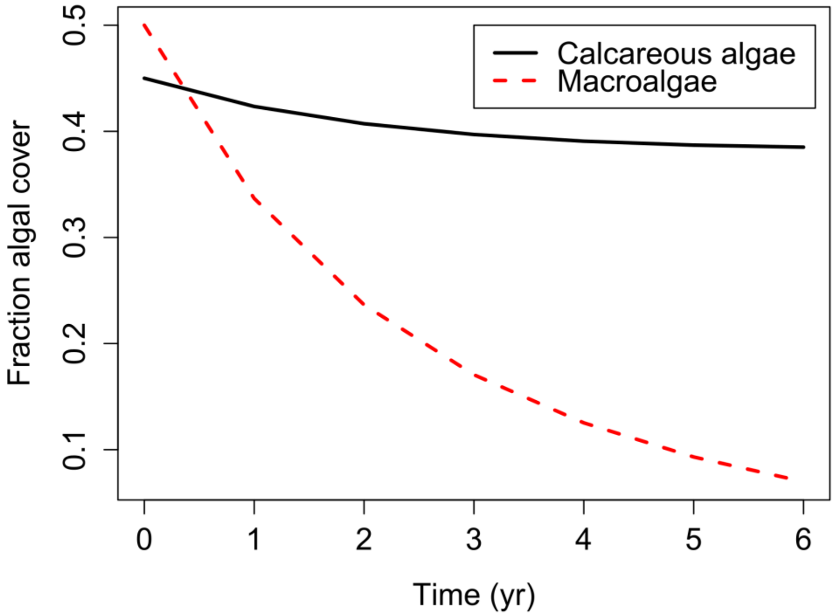

Figure 5 – Example of modelled algal coverage over time for calcareous algae (black line) and macroalgae (red dashed line). This corresponds to a 5 °C scenario where mALB of macroalgae was not obtained. The model parameters were set to g_C=0.03, g_M=0.3, k_{CM}=0.5, k_{MC}=0.5, d_C=0.01 and d_M= 0.5. Initial area coverage was 45 % for calcareous algae and 50 % for macroalgae. After less than two years, macroalgal cover was halved, to eventually reach zero. Calcareous algal cover stabilized around 40 %. This outcome, competitive exclusion of macroalgae, was most common when the mALB of macroalgae was not obtained.

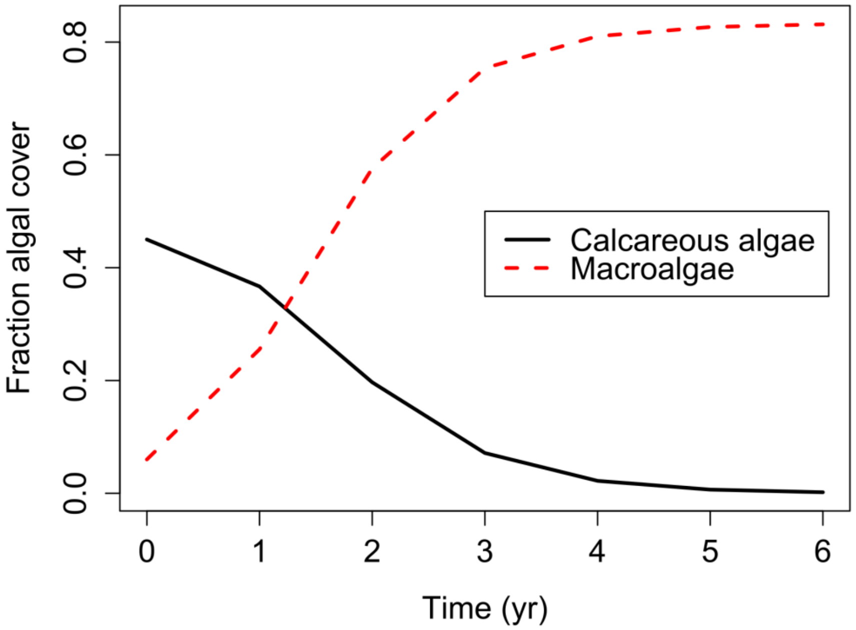

Figure 6 - Example of modelled algal coverage over time for calcareous algae (black line) and macroalgae (red dashed line). This corresponds to a 5 °C scenario where mALB of macroalgae was obtained. The model parameters were set to g_C=0.03, g_M=3, k_{CM}=0.5, k_{MC}=0.5, d_C=0.01 and d_M= 0.5. Initial area coverage was 45 % for calcareous algae and 6 % for macroalgae. After less than two years, macroalgae covered half of the available substrate, reaching and stabilizing around 80 % coverage. Calcareous algae were out-competed. This outcome, competitive exclusion of calcareous algae, was most common when the mALB of macroalgae was obtained.

3.2 TEMPERATURE EFFECTS

Generally, temperature increase did not change the macroalgae- or calcareous algae-dominance. Model outcomes did not differ greatly between the 0, 5 and 10°C scenarios (figure 7-10). Growth rate, *g* (which was temperature dependent), determined to a great extent the final abundance of the winning species; high growth rate gave high area coverage. The highest area coverage was reached at 10°C for *P. rubens* (90 %) and at 5°C for *Desmarestia spp*. (85 %). In two cases, at 10°C, the model gave rise to start dependent exclusion of macroalgae or calcareous algae (Figure 11A). When the mALB of *P. rubens* was not obtained and $k_{CM} = k_{MC} = 0.5$, *L. glaciale* outcompeted *P. rubens* if the initial area cover of *P. rubens* was low. Using the state in Smeerenburgfjord before year 2000, when macroalgae covered only less than 6 % (Kortsch et al., 2012) and calcareous algae around 45 %, as initial conditions, the model predicted that *P. rubens* would go extinct. However, if initial conditions were representative of the period after year 2000 (M = 20 %, C = 40 %) *P. rubens* eventually outcompeted *L. glaciale*. In both cases the transient time until the algae populations stabilized was long, about 100 years.

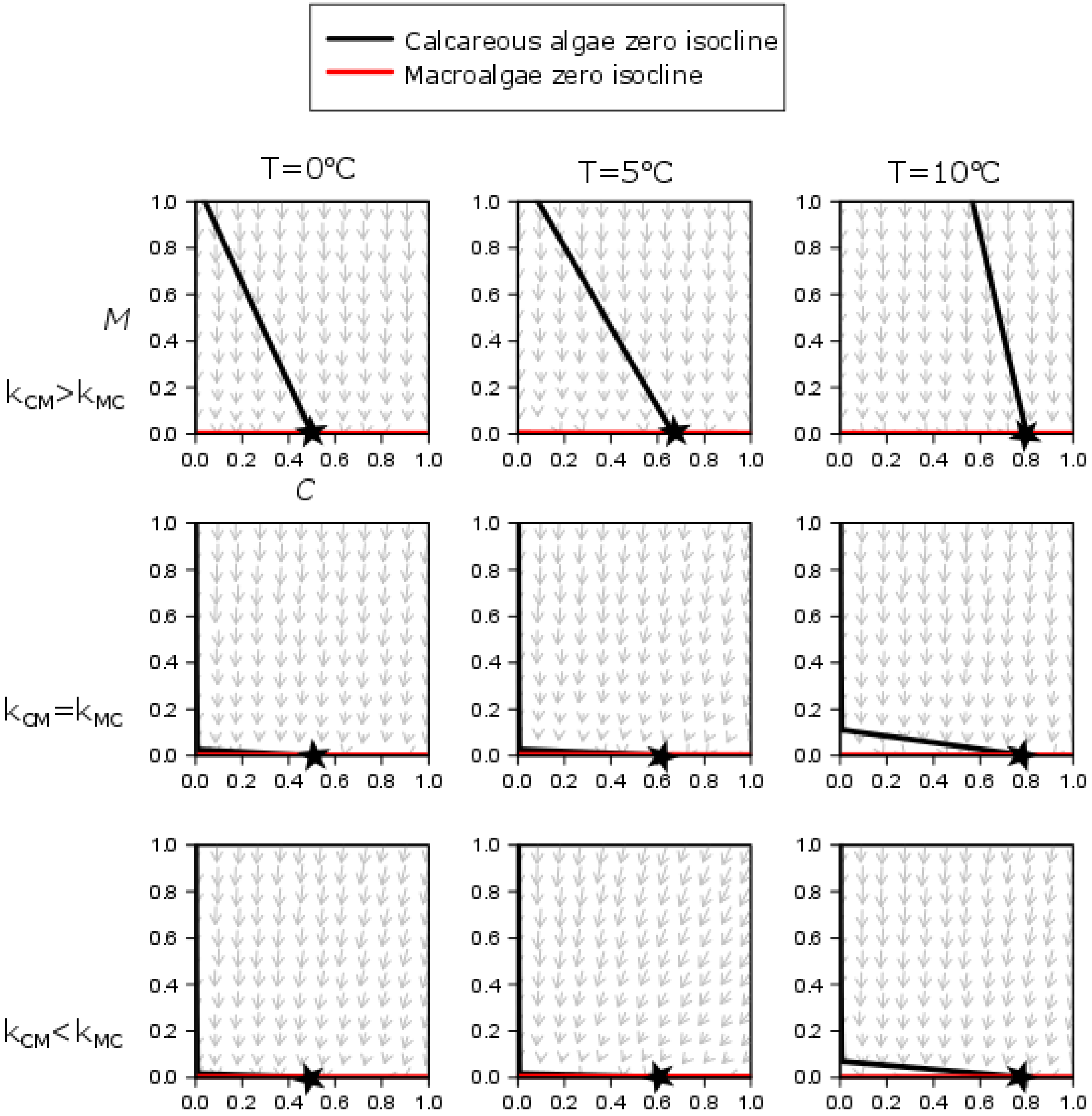

Figure 7 - Phase plane plots for *Desmarestia spp.* (*M*) and *L. glaciale* (*C*) when mALB was not obtained for *Desmarestia spp.* (annual light < 330 mol photons m^{-2} yr^{-1}). The diagrams show how the fraction of space occupied by calcareous algae (*C*, horizontal axis) and macroalgae (*M*, vertical axis) change at certain species combinations. The phase arrow direction indicate how *C* and *M* change at a certain point, the length of the arrows represent the rate of change, and the zero-isoclines represent the border at which the respective species populations does not grow or decrease (no net growth). Equilibrium points are marked with black stars. Since $g_M<d_M$ in all cases when annual light is low, the macroalgae could not establish and were out-competed independent of temperature, competitive ability and initial conditions. The final calcareous algae cover was mainly dependent on temperature (i.e. growth rate, g_M).

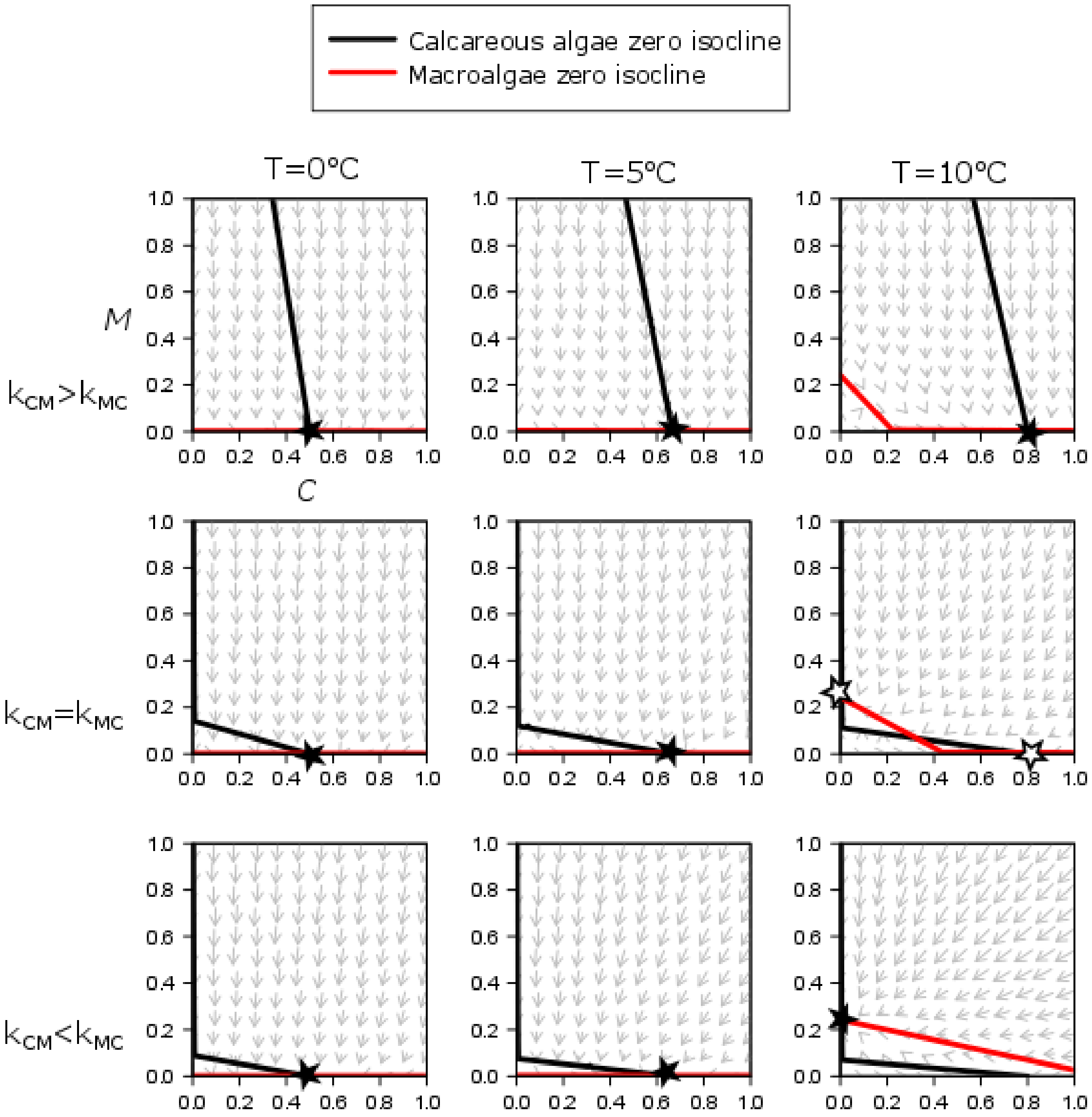

Figure 8 - Phase plane plots for *P. rubens* (*M*) and *L. glaciale* (*C*) when mALB was not obtained for *P. rubens* (annual light < 320 mol photons m^{-2} yr^{-1}). Equilibria are marked with black stars, and start-dependent equilibria by open stars. At low temperatures (0 and 5°C) the macroalgae could not persist and were out-competed independent of their competitive ability, *k*. At high temperature however, *P. rubens* could possibly establish. If $k_{CM}=k_{MC}=0.5$ the model produced start dependent exclusion. If $k_{CM}<k_{MC}$ *P. rubens* was found to out-compete *L. glaciale* and stabilized at around 25 % area coverage.

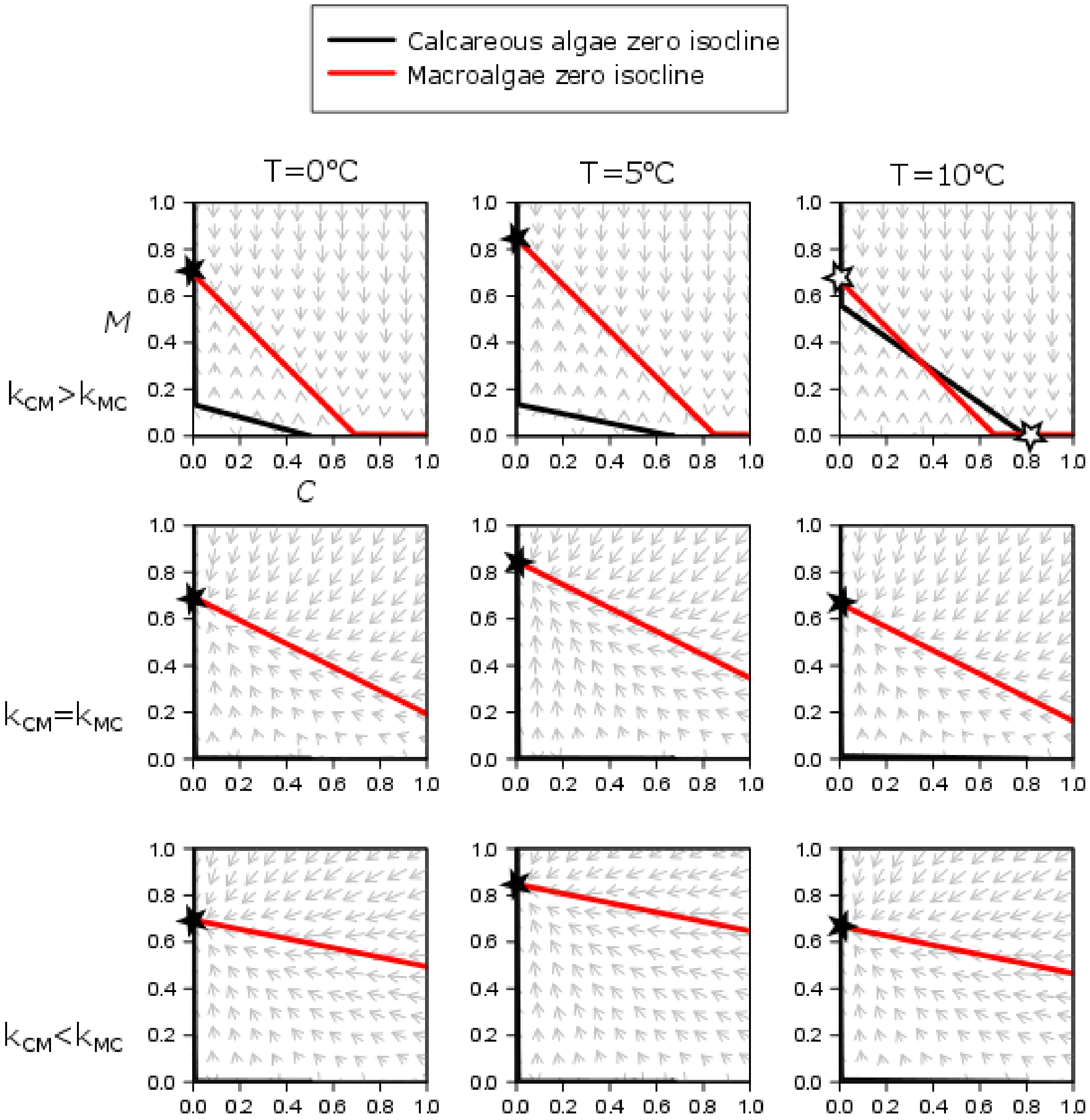

Figure 9 - Phase plane plots for *Desmarestia spp.* (*M*) and *L. glaciale* (*C*) when mALB of *Desmarestia spp.*was obtained (annual light >330 mol photons m^{-2} yr^{-1}). Equilibria are marked with black stars. In almost all cases, *Desmarestia spp.* would out-compete *L. glaciale*. The special case at $k_{CM}>k_{MC}$ and 10°C (upper right corner) shows start-dependent exclusion. This means that if calcareous algae cover was high from the start, calcareous algae out-competed macroalgae and vice versa. It can be pointed out that the *Desmarestia spp.* growth rate at 10 °C is lower than at 5°C.

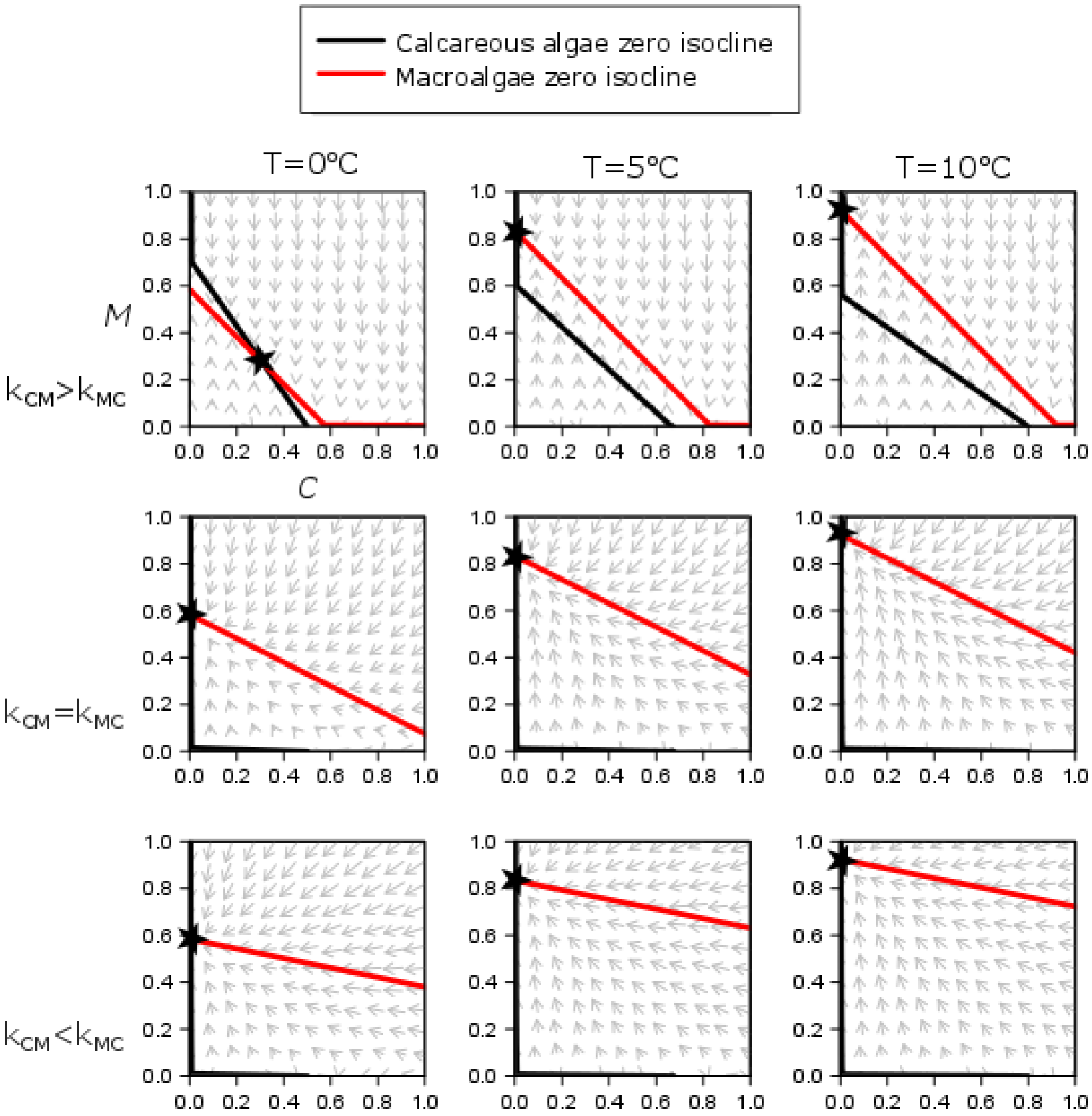

Figure 10 - Phase plane plots for *P. rubens* (*M*) and *L. glaciale* (*C*) when mALB of *P. rubens* is obtained (annual light >320 mol photons m^{-2} yr^{-1}). Equilibria are marked with black stars. The macroalgae out-competed the calcareous algae in almost all cases. However, when temperature was low (0°C) and $k_{CM}>k_{MC}$ (upper left plot) the model gave rise to stable coexistence between the two species. This outcome could be acquired in all cases when mALB was obtained, as long as k_{MC} was small enough in relation to k_{CM}.

3.3 COMPETITION

The competition coefficient values did not, in general, determine which of the two algae species dominated the simulated area. Only if the competitive ability of calcareous algae was much larger than that of macroalgae ($k_{CM}>>k_{MC}$) the model generated stable coexistence between the two algae types (Figure 11B). This outcome was possible although the mALB of the macroalgae species was obtained. For *L. glaciale* and *P. rubens* stable coexistence occurred at 0 °C (Figure 11B). The competing species then stabilized at almost equal area coverage (about 30-35 % for each species).

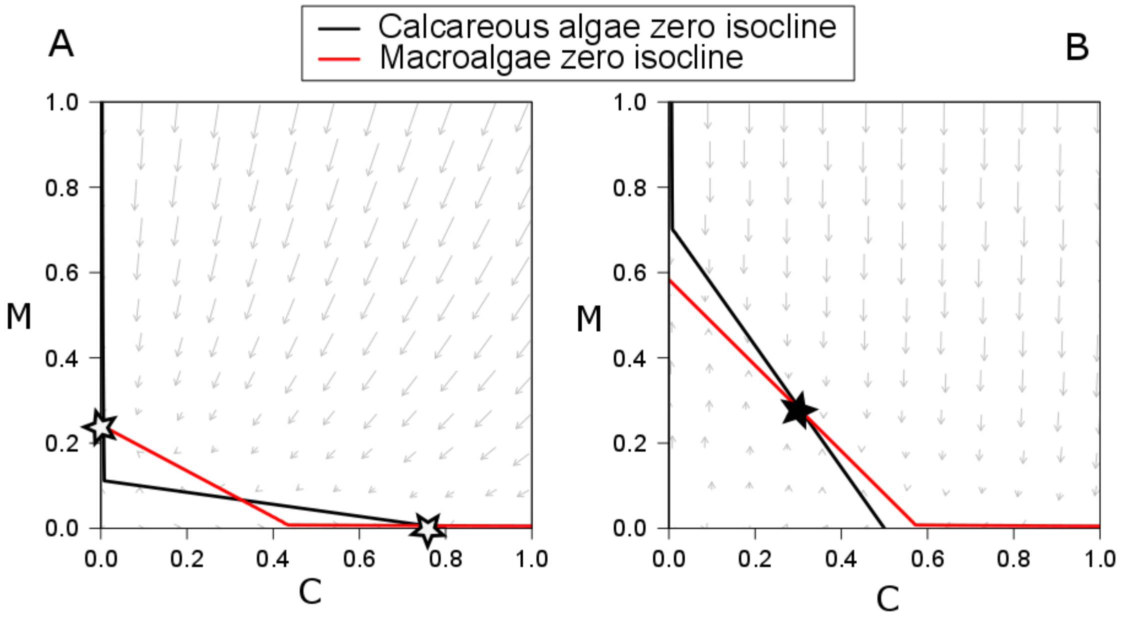

Figure 11 - Phase-plane plots showing how the fraction of space occupied by *L. glaciale* (*C*) and *P. rubens* (*M*) changes for two different scenarios. A) shows a 10°C scenario where mALB of *P. rubens* is not obtained, in which the outcome is dependent on the initial conditions (model parameter values correspond to: g_C=0.05, g_M=0.66, k_{CM}=0.5, k_{MC}=0.5, d_C=0.01, d_M=0.5). As long as *C* initially was high (above 35 %) and *M* was low (below 6 %) the macroalgae were outcompeted, but if the initial macroalgae cover was higher (above 30 %) calcareous algae were outcompeted. The open stars indicate the two possible equilibrium points, either a 75 % calcareous algae cover or a 25 % macroalgae cover. B) corresponds to a 0°C scenario where mALB of *P. rubens* is obtained and $k_{CM}>>k_{MC}$ (g_C=0.02, g_M=1.2, k_{CM}=0.9, k_{MC}=0.01, d_C=0.01, d_M=0.5). Here the model outcome was stable coexistence between the species, with about 30 % area coverage for both species, marked by a black star.

3.4 THRESHOLD FOR GROWTH RATE

Analysing the model outcomes from eq. 1 and 2 for different values of macroalgae growth rate, g_M, it was clear that a shift in macroalgae cover occurred as g_M exceeded a certain critical growth rate, g_{crit} (Figure 12). Algal growth rate, *g*, was in the model affected by both temperature and light conditions. Thus macroalgal growth rate increase, either through enhanced light conditions or increased temperature, could induce a theoretical regime shift.

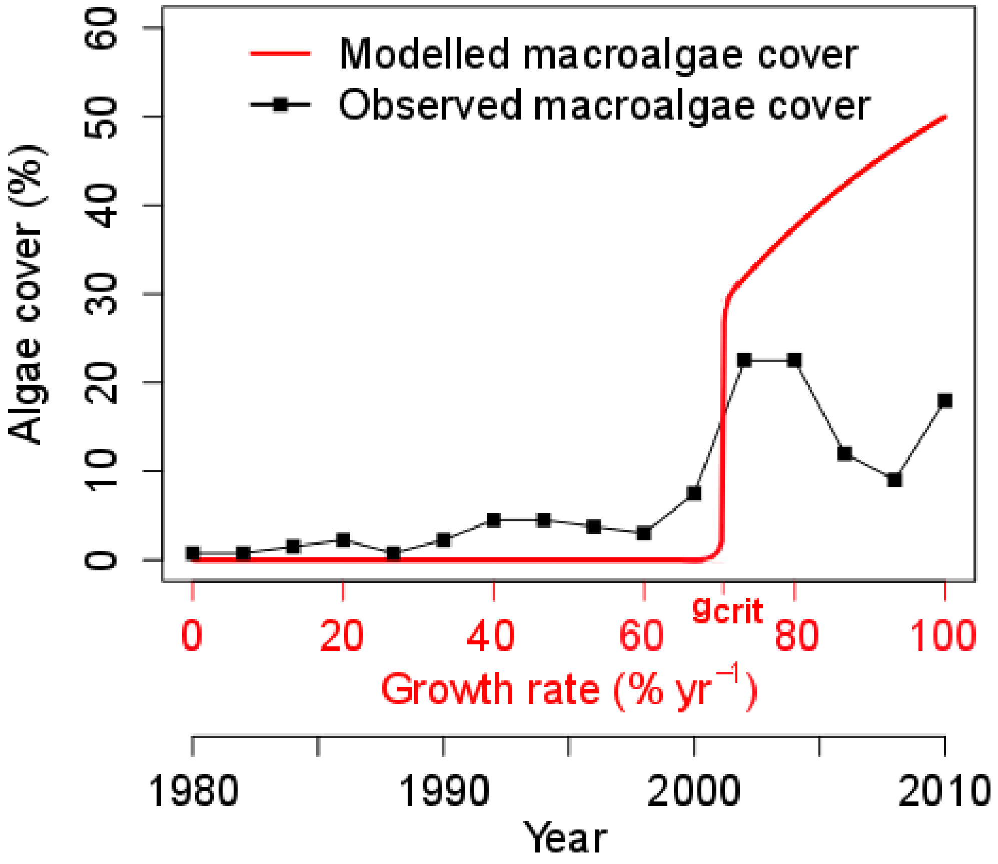

Figure 12 - Comparison of the modelled macroalgae (*P. rubens*, red line) cover for different growth rates, g_M, and the macroalgae cover observed by Kortsch et al. (2012) in Smeerenburgfjord, Svalbard (black squares). For the model output the parameters were set to g_C=0.05, k_{CM}=0.4, k_{MC}=0.6, d_C=0.01 and d_M=0.5. When g_M approached 70 % yr^{-1} macroalgae cover shifted rapidly, in resemblance with the documented shift in Smeerenburgfjord 2000.

4 DISCUSSION

The model approach showed that high macroalgal growth rates result in rapid expansion and complete dominance by macroalgae, unless the growth was limited by low light conditions. The non-linear increase of annual light that follows earlier sea-ice melt (Figure 4; Clark et al., 2013) and the threshold for algae growth characterized by the light compensation point, E_k, (Gómez et al., 2009) both support the suggestion that increasing light is the main cause for invertebrate-algae regime shifts. However, if light was the only factor limiting macroalgal expansion, one should have expected the shallow benthic communities in Svalbard to shift back and forth with the natural variations in sea-ice cover (Figure 2C) already back in the 1980's. Time delay in ecological response to change and life history of algae may to some extent explain the ecosystem stability before the regime shift. Biological and ecological feedback mechanisms were not incorporated in the simple model in this study, although they are known to stabilize ecosystem states and give rise to alternative stable states (further discussed in section 5.3). Thus feedback mechanisms could still be a contributing cause to regime shifts in Kongsfjord and Smeerenburgfjord.

4.1 EFFECTS OF TEMPERATURE, COMPETITION AND LIGHT ON ALGAE GROWTH AND COMMUNITY STRUCTURE

One crucial insight from the synthesis of algal growth rates made in this study is that the *in vitro* growth rates of the macroalgae are much greater, about 50-500 times higher (Adey, 1970; Bischoff and Wiencke, 1993; Novaczek et al., 1990), than the growth rate of coralline algae (i.e. $g_C << g_M$). Thereby, as long as light is not limiting for macroalgae growth, the most common model outcome is the one where macroalgae outcompete calcareous algae completely (Figure 6). Both coralline algae and macroalgae showed growth optima at relatively high temperatures (5-10 °C) (Adey, 1970; Bischoff and Wiencke, 1993; Novaczek et al., 1990). The studies providing the basis for my growth rate estimates did not, growth-wise, indicate better adaption to cold environments by the calcareous algae than by the macroalgae. Adding the fact that monthly SST in the waters northwest of Spitsbergen only varied between 1.0 and 5.5 °C during the period 1980-2010 (Kortsch et al., unpublished data), it seems unlikely that temperature changes and the temperature dependence of algae growth could be the sole cause of the shift in algal dominance. The macroalgal growth rates in this study were also consistently above the critical growth rate, g_{crit} (Figure 12). However, growth rates of the algae species are generally positively correlated with temperature at the temperature range in the north-western Svalbard area (Adey, 1970; Bischoff and Wiencke, 1993; Novaczek et al., 1990), underlining that temperature increase is a possible contributing factor to the ecosystem changes.

To generate coexistence between *M* and *C*, the large growth rate difference needed to be counterbalanced by other model parameters. Exploring the competition coefficient values, it was found that only for large differences in competition coefficients ($k_{CM} >> k_{MC}$) did the model show stable coexistence between *C* and *M* (Figure 11B). Low k_{MC} could be motivated by the manipulation experiment conducted in Smeerenburgfjord in the early 80's (Kortsch et al., 2012), where the reestablishment of species into a bottom transect cleared of organisms was monitored. The experiment showed that macroalgae only established and grew in areas cleared of calcareous algae, indicating that (under the prevailing environmental conditions) the expansion of macroalgae into space already occupied by calcareous algae was lower than its expansion into unoccupied space. For k_{CM} literature provides a mixed message; calcareous algae are seen as competitively inferior to overgrowers (Airoldi, 2000; Konar and Iken, 2005), indicating a low k_{CM}, but are also documented to survive overgrowth and even to continue to grow when covered (Dethier and Steneck, 2001). The manipulation experiment in Smeerenburgfjord supports the notion that calcareous algae can grow into space already occupied by macroalgae ($k_{CM} > 0$), since it was observed that calcareous algae eventually reclaimed dominance in the manipulated plot. The uncertainties concerning the competition coefficients make it desirable to clarify the overgrowth mechanisms and to obtain parameter values through competition experiments. However, the large difference between k_{CM} and k_{MC} needed to acquire stable coexistence in this study ($k_{CM} \approx 0.9$, $k_{MC} \approx 0.01$) may not be supported empirically.

Light conditions had a large impact on the model outcome; whether or not mALB of the macroalgae was obtained was critical for the species distribution. Although effects of light limitation on macroalgae growth, g_M, is uncertain, and the choice of a 90 % reduction of g_M as a consequence of light limitation based only on a one-algae experiment (Clark et al., 2013), the physiological properties of polar algae implies that light is a crucial factor. Polar seaweeds generally have low light requirements and only little light is needed to saturate the photosynthesis process (Gómez et al., 2009). This means that photosynthetic rate, and consequently growth rate, rapidly increases as the light compensation point is exceeded, implying that a small change in light regime can affect growth rate strongly.

Empirical evidence of light effects on macroalgae comes from Commonwealth Bay in Antarctica where a massive ice berg changed the climatic conditions in 2010, giving the previously ice-free area a year-round ice cover (Clark et al., 2015). The shallow (5-10 m) rocky-bottom ecosystem clearly responded to this sudden decrease in annual light; all observed macroalgae were categorized as either decomposing (78 %), discoloured (20 %) or bleached (2 %) three years after the ice berg event (calcareous algae however were not as severely affected) (Clark et al., 2015). These observations support a strong decrease in g_M, or large increase in d_M, when mALB is not obtained. Moreover, since light attenuates strongly in water, light effects on the community scale can be seen through looking at the depth distribution of benthic algae. In Svalbard calcareous algae dominate rocky-bottom areas at greater depths (30-80 m) with up to 100 % coverage of available substrate, while erect macroalgae increase in abundance with decreasing depth (< 30 m) (Teichert et al., 2013). This underlines the importance of light conditions for limiting macroalgae growth.

4.2 COMPLIANCE WITH OBSERVATIONS IN KONGSFJORD AND SMEERENBURGFJORD

Due to the simplified approach, model results in this study differ in many aspects from the observations made in Kongsfjord and Smeerenburgfjord. Generally, the model proposes total competitive exclusion of one species although calcareous algae and macroalgae coexist in the two fjords, both before and after the shifts. When parameter settings do produce stable coexistence or start-dependent exclusion the time until populations stabilize can be long (up to 100 years) and the model cannot follow the fluctuations in macroalgae cover documented in the fjords after the shifts (Figure 12, Kortsch et al., 2012). Also, the modelled species abundances differ somewhat from observations. However, the aim of this study was to explore the underlying mechanisms behind invertebrate-algae shifts, not to accurately predict algae cover as a function of environmental conditions and time. Consequently, when the mode e.g. predicted competitive exclusion of macroalgae, it was interpreted as calcareous algae dominance but not necessarily as total exclusion of macroalgae.

In general seasonality and timing was not recognized in this year-based model although it could be crucial for algal expansion. Predicting for example monthly changes in algal coverage would require much more detailed information about algal life cycles and incorporation of monthly light and temperature data, which would be time consuming, but far from impossible. However, most importantly, the results would be impossible to validate against observations. The low time resolution and limited precision (based on biannual photographic surveys) of the data from Kongsfjord and Smeerenburgfjord, with which the model results are compared, motivates a simple model structure and a qualitative rather than quantitative interpretation.

In scenarios where macroalgae dominated, both *Desmatrestia spp.* and *P. rubens* reached high abundances (60-90 %) (Figure 9Figure 10). This can be compared to the observed average macroalgae cover after the shifts; 40 % in Kongsfjord and 26 % in Smeerenburgfjord (Kortsch et al., 2012). For calcareous algae dominance the predicted calcareous algae cover (50 to 80 % depending on growth rate/temperature (Figure 7Figure 8)) was in better accordance with the situation in Kongsfjord and Smeerenburgfjord (about 65 and 45 % respectively before the shifts (Kortsch et al., unpublished data)). One reason why predicted algae cover is generally higher than the observed is that *in situ* the presence of other species affects algae distribution. In Kongsfjord and Smeerenburgfjord a total of 23 and 36 benthic taxa have been recorded (Kortsch et al., 2012), naturally decreasing the available space. Moreover, grazing is an important control mechanism for algae expansion not accounted for in the model formulation. The calcium carbonate skeleton of calcareous algae is considered important as grazing protection (Adey et al., 2013) and calcareous algae often dominate in areas with high grazing pressure (Steneck, 1986; Steneck and Dethier, 1994). Morevoer, the importance of sea urchin grazing on *Desmarestia spp.* has been documented in shallow benthic communities in eastern Canada (Blain and Gagnon, 2014). This could explain why the model compliance was higher for calcareous algae than for macroalgae, and further development could include grazing effects either in parameter values or through adding an herbivore to the model.

Perturbations are considered important for coexistence in shallow benthic communities, and the notion that intermediate disturbance promotes biodiversity in shallow rocky-bottom ecosystems, through reducing competitive exclusion, has been supported in several studies (Dayton and Hessler, 1972; Lubchenco, 1978; Paine, 1984; Paine and Vadas, 1969). Although physical disturbance (e.g. waves, ice scour and tidal action) generally decreases with depth, these events together with biological disturbance such as grazing and disease affect subtidal communities like the ones in Kongsfjord and Smeerenburgfjord, partly explaining the diversity at the sites. Disturbances are generally stochastic, but the model used in this study is strictly deterministic, meaning that populations will stabilize at a certain size and that the outcome for a certain parameter setting always will be the same. This feature of the model, apart from the large differences in algal growth rates, explains the high incidence of competitive exclusion. Interestingly, although the model predicted competitive exclusion of calcareous algae at high light and temperature conditions, calcareous algae cover in Kongsfjord and Smeerenburgfjord remained relatively stable after the shifts in 1995 and 2000 (Kortsch et al., unpublished data). This highlights a shortcoming in the choice of model structure;

the two-dimensional output does not account for the fact that erect macroalgae to some extent float above the bottom, and that calcareous algae can tolerate both direct overgrowth and shading (Dethier and Steneck, 2001; Miles and Meslow, 1990). Therefore it could be appropriate to modify the model, either allowing two species to occupy the same space, or using a model that produces output with a two-layer structure.

At a certain macroalgae growth rate, the model implied a shift from calcareous algae to macroalgae dominance. The critical growth rate for a warm (≥5 °C) scenario was around 70 % yr^{-1} (Figure 12) while macroalgae growth rates are considerably higher, ranging between 120 and 1400 % yr^{-1} (Table 1). There are however several reasons to be flexible when it comes to the growth rate values. Annual growth, *g*, was determined through summing the *in vitro* growth rate over an estimated growing season, but for *P. rubens* growth rate varies over the growing season and with plant age (Schoschina, 1996). Similar variations in growth pattern most likely also exist in *L. glaciale* and *Desmarestia spp*.. Not all growth results in extension of the area coverage, since algae might need to allocate energy for wound healing or increasing the thallus or crust thickness, and macroalgae growth rate describes the vertical as well as horizontal expansion in space. Therefore it is likely that the *in situ* growth into unoccupied space is lower than the *in vitro* growth rates used in this model. Another aspect of algal growth, not reviewed in this study, is the temperature dependence of reproduction. In the model formulation by Crowley et al. (2005) an expansion coefficient, including both growth of tissue and different reproduction methods, is used instead of the algal growth rate, *g*. Earlier studies indicate that e.g. calcareous algae require low (2-3°C) winter temperatures for reproduction (Adey, 1973) and that they can reproduce while overgrown (Miles and Meslow, 1990). Therefore, adding a reproduction rate the model should be considered in future studies.

4.3 ALGAE REGIME SHIFTS – IRREVERSIBLE CHANGE OR LIGHT DRIVEN NON-LINEAR BEHAVIOUR?

The distinct differences between community structure and dynamics before and after 1995-1996 and 2000 in Kongsfjord and Smeerenburgfjord are indicative of regime shifts where benthic communities passed from one state to another (Kortsch et al., 2012). However, the nature of the shifts in terms of stability and reversibility remains elusive. A light-driven regime shift in polar marine ecosystems can be of three different kinds (Figure 13). We can define the ecosystem state (*S*), here ranging from high calcareous algae cover to high macroalgae cover, responding to changes in a driver (*D*), here ranging from low to high annual light. Assuming that the state is a linear function of the driver (Figure 13A), an ecosystem shift can only occur if the driver increases substantially (*dD* is large). However, if the state is a non-linear function of the driver (Figure 13B), a small change in driver (small *dD*) could be enough to cause a large shift in state. Lastly, the state can exhibit hysteresis (Figure 13C), meaning that there are two alternative stable states for a certain driver range. In this case, the ecosystem state can be either along the lower or upper solid line, while the dashed line indicates an unstable equilibrium. A small increase in driver (or a perturbation) can force the ecosystem to tip over into a new state, but a corresponding decrease will not bring the system back to its original state.

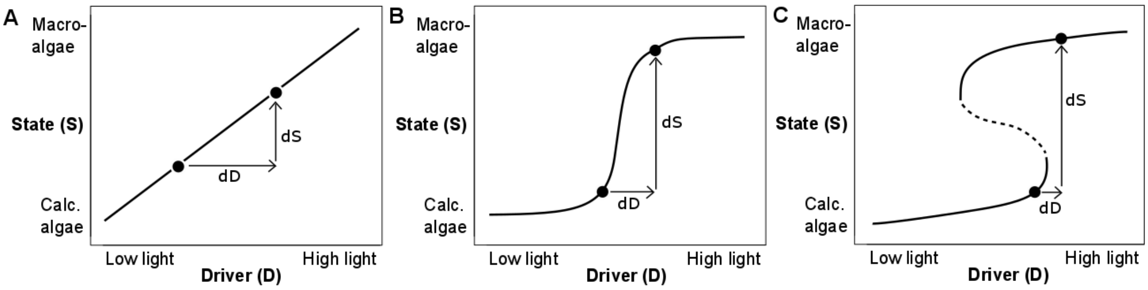

Figure 13 - Three possible mechanisms behind light-driven regime shifts in partly ice-covered marine systems, describing how the ecosystem state (*S*) is affected by changes in driver (*D*). For the benthic communities in this study, the level of calcareous vs. macroalgae dominance is assumed to be a function of light and the black points represent the states before and after a shift. A) The response of the state to changes in driver is linear, meaning that only a large shift in light, *dD*, can produce a large shift in state, *dS*. (B) The response of the state to changes in driver is non-linear, thus a small *dD* can cause a large *dS*. (C) The relation between *D* and *S* is non-linear and discontinuous, implying that a small *dD* may cause a large *dS*, and that the shift in state is difficult to reverse; if the ecosystem gets pushed into the state with high macroalgae abundance by a small increase in light, the system reaches an alternative state and follows the upper solid line. A corresponding decrease (*dD*) in light will then not make the system go back to its earlier state.

As concluded in this study, and by Clark et al. (2013), the timing of sea-ice melt in relation to the annual solar cycle can cause non-linear behaviour of annual light in partly ice-covered marine systems. By a gradual warming and gradually decreasing ice-cover, this can cause a substantial change in light regime (large dD, Figure 13A). Moreover, the physiology of benthic algae implies a threshold effect on the macroalgal response to light increase. This non-linear response of the state (Figure 13B) could also explain the tipping-point dynamics since a small increase in light (small *dD*) can create a large shift in algae dominance (*dS*). Common to these two scenarios is that the shifts are reversible; a corresponding decrease in light will take the benthic community back to its original state. Combining the two mechanisms, there is strong theoretical support for the view that algae shifts in shallow polar benthic communities are driven by changes in light and that they are reversible.

However, the community structure at the investigated sites in Kongsfjord and Smeerenburgfjord was relatively stable before the shifts in 1995-1996 and 2000, despite fluctuations in both sea surface temperature and length of the ice-free season. Even after the manipulation experiment performed in Smeerenburgfjord in the 80’s, where the communities were strongly perturbed through removal of all organisms from a bottom transect, the community returned to its original state within 6 years (Kortsch et al., 2012 supporting information). It is possible that the macroalgal life cycles require several consecutive years of favourable light conditions at the right time of the year to expand, explaining, in part, some of the system stability. Some ecological systems can exhibit time lag in the response to changes (Gray and Christie, 1983; May, 1973). This could also explain why the benthic community did not respond directly to changes in environmental conditions; the shifts occurred some years after a peak in ice-free period (Figure 2C). Lastly, ice conditions in fjords in western Spitsbergen show large inter-annual variability (Cottier et al., 2007; Gerland and Renner, 2007) and are affected by local factors such as wind and weather patterns, fjord morphometry and glacier melt (Svendsen et al., 2002). It is therefore not certain that the length of the ice-free period at the sites coincided with the regional average.

The stability of the community structure before the shifts also supports the notion that the ecosystem previously resided in a stable state, characterized by low macroalgal abundance. Positive feedback mechanisms then kept the system in its state despite variations in climate and perturbations. Generally, if external drivers change sufficiently, a system can tip over into an alternative stable state (Beisner et al., 2003; Scheffer and Carpenter, 2003) which is in turn preserved by other positive feedback mechanisms (Folke et al., 2004). If this is the case in Kongsfjord and Smeerenburgfjord, the algae shift may not be reversed although light is reduced again. A relevant parallel to the regime shifts in Arctic benthic ecosystems is the regime shifts from coral to algae dominated state recorded in the tropics (Bellwood et al., 2004). Coral-algae regime shifts have been driven by a combination of increased nutrient loading and alterations in the abundances of keystone species (Mumby et al., 2006) and these systems show hysteresis (Bellwood et al., 2006); the pathway back from an algae dominated state is not the same as the way there (Figure 13C).

In contrast to the coral-algae shifts, invertebrate-algae regime shifts occur in areas where light is limiting. Despite acknowledging the importance of positive feedback mechanism in preserving the invertebrate-dominated state, this study suggests that the shifts in Kongsfjord and Smeerenburgfjord are likely reversible, as light is an important structuring force for macroalgae-dominated communities. The empirical evidence of the macroalgal decline following a sudden increase in sea-ice cover in Antarctica (Clark et al., 2015) supports this view, although in that case, ice conditions shifted from almost no sea-ice to an all-year ice cover. In the present case study systems, the change in sea-ice cover over time has not been as dramatic.

4.4 MODEL LIMITATIONS

The simple model used in this study cannot exhibit hysteresis (Figure 13C). The model includes interspecific competition, an interaction that can give rise to complex dynamics in community models (Molis and Gama, 2009), but lacks components such as density dependent algae growth and herbivore-plant interactions. Moreover, since stability and ecosystem resilience may increase with functional diversity (Hooper et al., 2005; Ives and Carpenter, 2007; Peterson et al., 1998) and food-web complexity (Dunne et al., 2002; Harding, 1999) it is apparent that a two-species, single trophic level model will not capture the whole ecosystem dynamics. It can seem desirable to include more realism in future models to better explore the tipping-point dynamics of the studied ecosystems, but it is important to consider the difficulties with parameterization of complex mechanistic models. In this case, algal death rates and competition coefficients were difficult to determine from literature, and would be time consuming to determine experimentally. To quantify additional biological and ecological parameters and include more species is a challenge, especially considering the lack of empirical data from arctic marine systems (Wassmann et al., 2011).

4.5 RECOMMENDATIONS FOR FUTURE STUDIES

A simple model, like the one used in the current study, can give qualitative insights into ecosystem behaviour and be compared with the more complex reality, providing a framework that may guide experimental design (Odenbaugh, 2005). To increase model realism, it is recommended that grazing and recruitment be incorporated in the model formulation. Grazing could be modelled either as an additional species, or included in the algal death rate. The temperature dependence of reproduction could be further investigated in future studies. Another relevant adjustment could be to allow shared space in the model, since it is possible for calcareous algae to survive overgrowth by macroalgae. Moreover, positive feedback mechanisms such as density dependent growth and facilitation, necessary for establishing critical thresholds, could be included in the model to investigate if the shallow rocky-bottom ecosystems in question display alternative stable states within a relevant parameter space.

Some experimental work is suggested based on the current study. Competition coefficients for macroalgae and calcareous algae could be determined experimentally to improve model parametrization. Considering this study's emphasis on light as a driver of change, it would also be relevant to perform shading experiments on the community level. Since local light data is lacking, an empirical study could address the importance of light for community structure and determine the reversibility of invertebrate-algae regime shifts in the Arctic.

5 CONCLUSIONS

The compilation of algae properties and parameter estimates proposed in this study has created a more substantial basis for evaluating the dynamics of benthic algal species in the Arctic, and for analysing changes in benthic community structure in relation to climate warming. Change in light regime was identified as the main trigger of regime shifts in shallow, seasonally ice-covered benthic communities. The physiological threshold effect for macroalgal growth, the high macroalgal growth rate at ambient temperatures, and the non-linear increase in annual light that accompanies a prolonging of the ice-free season suggest that the documented regime shifts could be purely light driven. This is in contrast to the proposed explanations for coral-algae shifts at lower latitudes, and has implications for the reversibility and dynamic behaviour of regime shifts in arctic marine benthos. In a greater perspective, it highlights the importance of a mechanistic understanding of the ecosystem that undergoes a regime shift.

The documented regime shifts in Kongsfjord and Smeerenburgfjord are likely to be reversed if the length of the ice-free period decreases. However, considering the current development with a strongly declining arctic sea-ice cover (Comiso et al., 2008) and projections of an ice-free summer before 2050 (Wang and Overland, 2009), a reversal to the previous community structure at the sites on western Spitsbergen seems unlikely. Rather, similar regime shifts from invertebrate- to macroalgae-dominated ecosystem states can be expected in the whole arctic region.

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APPENDIX

A1 GROWTH RATE ESTIMATION

L. glaciale: specimens from the Tromsö area, 5-20 m depth, ambient summer temperatures about 5-8°C. g_C (% yr^{-1}) was calculated as the yearly area increase for a circular plant of initial diameter 10 cm (Irvine and Chamberlain, 1994; Suneson, 1943), marginal expansion 4, 9 and 12 µm day^{-1} and growth period 6 months (Adey, 1970).

P. rubens: specimens from the North Atlantic Ocean (Canada and France) (Novaczek et al., 1990). Growth was measured as increase in thallus surface area at two different irradiance levels. gM (% yr^{-1}) at 0, 5 and 10°C was estimated as the mean value of the growth rates of the two Canadian and three European isolates for the higher irradiance level, assuming a growth period of 4 months per year (Schoschina, 1996).

Desmarestia spp.: specimens from Disko Island (Greenland) (Bischoff and Wiencke, 1993), an area with ambient spring temperature -2 – 5°C (Heide-Jørgensen et al., 2007). The daily specific growth rate was measured in biomass increase and thus gM (% yr^{-1}) was estimated as the sporophyte growth rate (Bischoff and Wiencke, 1993) during a 4 months growth period (Blain and Gagnon, 2013).

A2 IRRADIANCE MODEL

Beer-Lambert's law was used to estimate the summed annual light budget at the depth of the sites (15 m) in Kongsfjord and Smeerenburgfjord. PAR irradiance data from Rijpfjorden (Nordaustlandet, Svalbard), collected between January 25th and October 23rd was used in the light model. The light intensity, E_z, at depth z was calculated as:

$$E_z = E_0 e^{-k_d z} \qquad \text{eq. A1}$$

where k_d is the light attenuation coefficient and E_0 the irradiance at the sea surface.

Equation A1 was used to calculate the annual light budget in Rijpfjorden as a function of depth. Light attenuates non-linearly with depth, meaning that annual light decreased rapidly the first 5-10 meters (Figure A1). The light attenuation coefficient determines the shape of the curve. For clear water conditions (kd = 0.1), the annual light budget at 30 meters depth was 240 mol photons m^{-2} yr^{-1}. This is below the annual light budget threshold of 252 mol photons m^{-2} yr^{-1} used by Clark et al. (2013) to distinguish between potential invertebrate and macroalgal habitat, indicating that this depth is a natural lower limit for macroalgae dominated communitites in northern Svalbard.

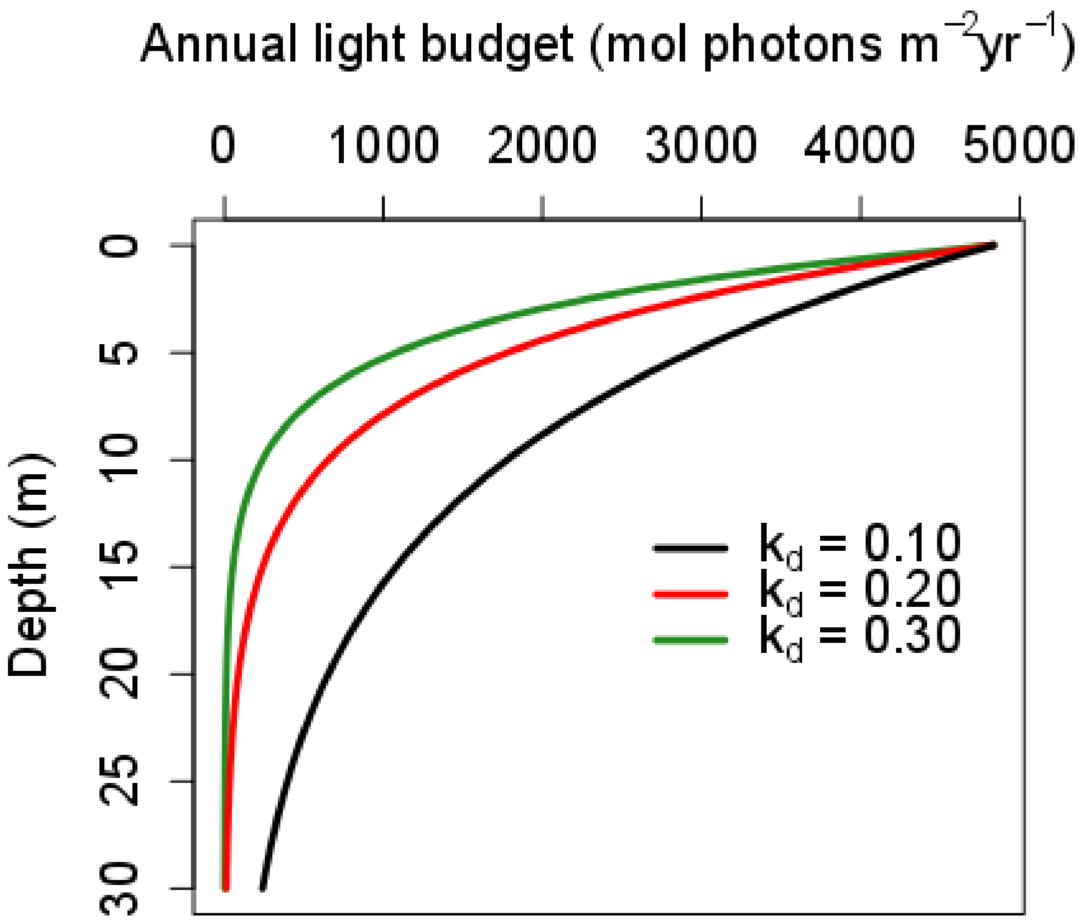

Figure A1 - Theoretical annual light budget as a function of water depth in Rijpfjorden. If the light attenuation coefficient is low (0.10) the annual light budget at 30 m depth is 240 mol photons m^{-2} yr^{-1}, below the annual light budget threshold of 252 mol photons m^{-2} yr^{-1} used by Clark et al 2013 to distinguish between potential invertebrate and macroalgal habitat.

A3 mALB CALCULATIONS AND SOURCES

The minimum annual light budget, mALB, for *Desmarestia spp.* was calculated from the mean value of the E_c values in the two studies by Kühl et al. (2001) and Johansson and Snoeijs (2002). For *P. rubens* mALB was determined as the mean of the value given by Johansson and Snoeijs (2002) and the two (summer-autumn and winter-spring) values given by King and Schramm (1976). E_c for *L. glaciale* was not stated by Adey (1970) but since growth was recorded at 4.2 µmol phot. m^{-2} s^{-}1 but not at 1.6 µmol phot. m^{-2} s^{-1}, the light compensation point was estimated as the value in between. Burdett et al. (2012) measured the light saturation point (E_k) for *L. glaciale*, and in accordance with Cole and Sheath (1990) it was estimated that $E_c = E_k/20$.

Table A1 - Summary of the E_c values used for determining the mALB for *Desmarestia spp.*, *P. rubens* and *L. glaciale*.

Algae species	**E_c (µmol phot. m^{-2} s^{-1})**	**mALB (mol phot. m^{-2} yr^{-1})**	**Reference**	**Comment**
Desmarestia aculeata	4.1	130	Kühl et al 2001	Lab experiment, samples from NE Greenland, around -0.5 °C.
Desmarestia aculeata	17*	537	Johansson and Snoeijs 2002	Skagerrak and Baltic Sea, summer lab experiments, 14 °C
Phycodrys rubens	11*	348	Johansson and Snoeijs 2002	Skagerrak and Baltic Sea, summer lab experiments, 14 °C
Phycodrys rubens	5 and 14	158 and 442	King and Schramm 1976	W Baltic, higher value corresponds to summer-autumn, lower value to winter-spring. 5, 10, 15 and 20 °C for winter, spring, autumn and summer.
Lithothamnion glaciale	1.6 - < 4.2	51-132	Adey 1970	Samples from Tromsö vicinity collected from 5-20 m depth in October, then treated with monthly realistic water temperatures. At 1.6 µmol phot. m^{-2} s^{-1} no growth was recorded at 10 °C while at 4.2 growth was recorded at 0-10 °C.
Lithothamnion glaciale	< 4.5-54.6	7-85**	Burdett et al. 2012	Both field and lab observations. E_k was variable, 4.45 to 54.61. E_c is lower than these values. 7-12 °C. E_k was generally lower in lab than in field.

* Values determined during the same experiment

** Light compensation point estimated as Ec = E_k/20 (Cole and Sheath, 1990)