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Ecophysiological Responses of Sea Ice Algae and Phytoplankton to a Changing Arctic

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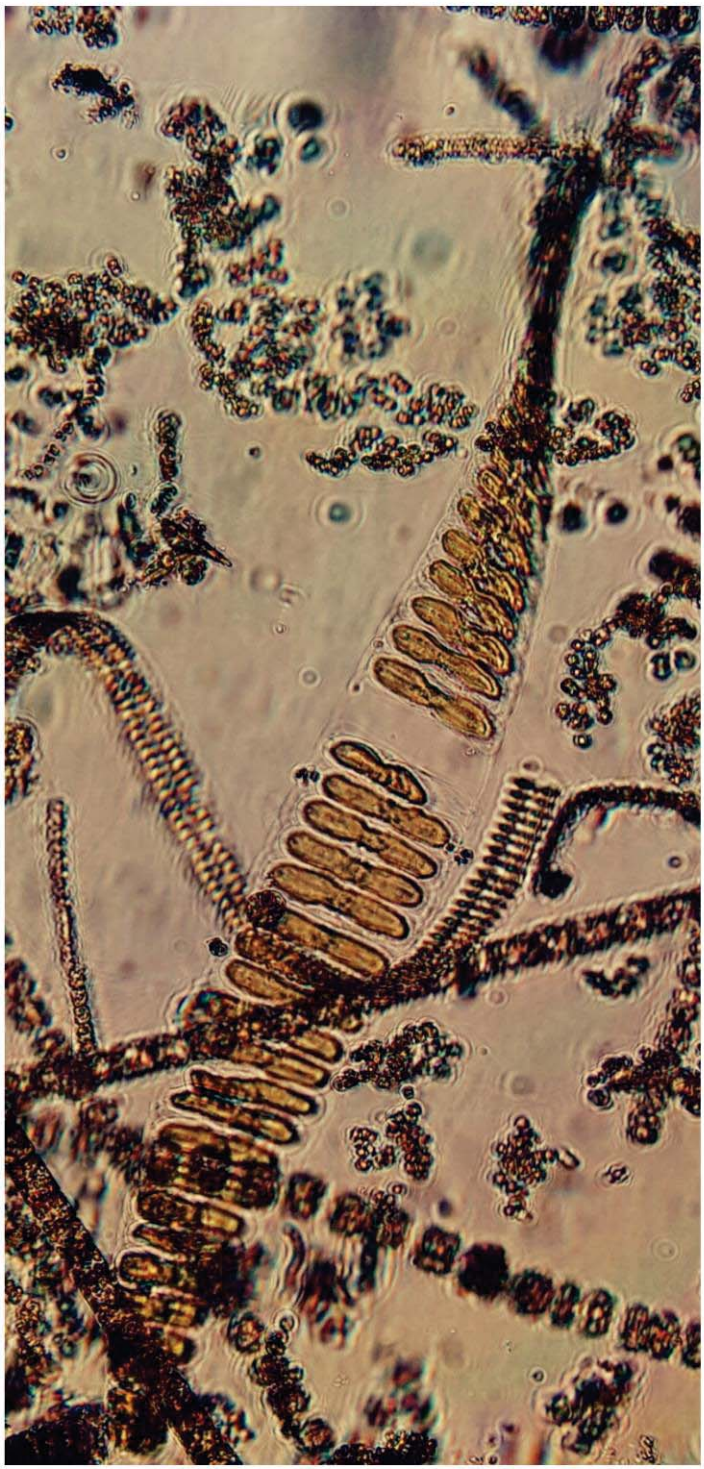
Ane Cecilie Kvernvik

A dissertation for the degree of Philosophiae Doctor – January 2019



Ecophysiological Responses of Sea Ice Algae and Phytoplankton to a Changing Arctic

Ane Cecilie Kvernvik

Dissertation submitted in partial fulfillment of the requirements for the degree of

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“It seems to me that the natural world is the greatest source of excitement; the greatest source of visual beauty; the greatest source of intellectual interest. It is the greatest source of so much in life that makes life worth living.”

— David Attenborough

“*No matter how politely one says it, we owe our existence to the farts of blue-green algae”*

— Diane Ackerman

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Ane Cecilie Kvernvik, Longyearbyen, January 2019

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Abstract

The ice-covered seas of the Arctic have two major types of primary producers; phytoplankton growing in open waters and sea ice algae growing within and on the underside of the sea ice. This thesis investigates the controlling role of light availability on Arctic pelagic and sympagic (i.e. ice-associated) algae, and how light-induced responses are modulated by NO_3 and pCO_2 levels. A combination of field sampling, *in situ* experimental studies, and laboratory experiments were performed in order to investigate photophysiological and biochemical characteristics of pelagic and sympagic algae and identify their respective responses to changes in their abiotic environment. The results revealed that in both pelagic and sympagic algae, a change in light availability exerted stronger control on physiological characteristics than variations in NO_3 and pCO_2 levels. Pelagic algae have evolved pronounced mechanisms into being flexible with different irradiances they encounter. Even though the ambient light during the polar night was not enough to support any measurable net primary production, they maintained an active photosynthetic apparatus, which ensured a fast recovery and utilization of even very low constant irradiances upon re-illumination. Furthermore, they effectively exploited very low irradiances for carbon fixation, handled instantaneous light stress well, and exhibited high photoacclimative capacity towards increasing irradiances. Pelagic algae also showed high resilience towards changing nutrient and pCO_2 levels. In conclusion, these results imply a high capacity of pelagic algae to compensate for changes in their abiotic environment. Sympagic algae also efficiently harvested low irradiances for light-dependent photosynthesis. However, they probably used more of the photosynthetic resources for tolerating extreme physico-chemical properties within sea ice, which resulted in lower rates of carbon assimilation compared to pelagic algae. Sympagic algae also showed higher sensitivity towards high light than pelagic algae, where the highest irradiances caused dysfunctional photophysiology and reduced fitness of the former. Moreover, they exhibited higher sensitivity towards a combination of multiple stressors. The Arctic ocean is changing fast in many respects, amongst which increased light regimes, stratification, and ocean pCO_2 levels stand out as being very important for microalgal communities. The results of this study suggest that sea ice algae will struggle more with adapting to the expected environmental changes compared to phytoplankton. We therefore anticipate a change in sea ice-based vs. pelagic primary production with respect to timing and quantity in a future Arctic, with potentially cascading effects on downstream food webs. The clearly distinct responses of pelagic vs. sympagic algae to environmental differences also need to be incorporated into model-based scenarios of future Arctic algae blooms and considered when predicting implications for the entire ecosystem.

List of papers

This thesis is based on the following three papers, referred to as **Paper I-III** in bold throughout the text.

Paper I:

Kvernvik AC, Hoppe CJM, Lawrenz E, Prášil O, Greenacre M, Wiktor JM, Leu E. 2018. Fast reactivation of photosynthesis in Arctic phytoplankton during the polar night. *Journal of Phycology* **54**:461-470. DOI:10.111/jpy.12750

Paper II:

Kvernvik AC, Hoppe CJM, Greenacre M, Verbiest S, Wiktor JM, Gabrielsen TM, Reigstad M, Leu E. Arctic sea ice algae differ markedly from phytoplankton in their ecophysiological characteristics. *Manuscript in preperation for submission.*

Paper III:

Kvernvik AC, Rokitta SD, Leu E, Harms L, Gabrielsen TM, Rost B, Hoppe CJM. In review. Higher sensitivity towards light stress and ocean acidification in an Arctic sympagic compared to a pelagic diatom. *Submitted to New Phytologist*.

Section I

Synthesis

Chapter 1

Introduction

1.1 Thesis outline

This thesis is divided into two sections. Section I includes 5 chapters giving an overview of the PhD thesis. Chapter 1 provides a general introduction as well as the objectives and scope of the thesis. Chapter 2 describes the study area and methods used during the PhD study. A general overview of main findings from research **Paper I, II and III** are presented in chapter 3, and chapter 4 discusses these findings. Conclusions are described in chapter 5, followed by a list of references used in section I in chapter 6. Section II consists of the three research articles.

1.2 Background

Arctic primary production

Primary productivity in the Arctic is characterized by large temporal and spatial variability on various scales, due to the extreme seasonal change in light availability and annual expansion and melt/decrease of sea ice. The polar night at high latitudes is characterized by long periods of continuous darkness and has been considered a period of limited biological activity. Recent studies, however, challenge this paradigm, as they reveal relatively high winter activity at several trophic levels (Berge *et al.,* 2015a, 2015b). In fact, despite the lack of photosynthetic activity during the darkest period of the year, many Arctic phototrophic algae are able to persist during the polar night as viable and active cells (Vader *et al.,* 2014, Kvernvik *et al*., 2018). Some organisms are known to switch to a heterotrophic lifestyle when the light is limiting and others produce spores and cysts to survive the winter (Jones 2000, Figueroa *et al.,* 2011). Following the suns return in early spring, a first algal growth takes place in the bottom layer of the sea ice, and during the transition to permanent light exposure, sea ice communities are thought to pass three distinct phases (Fig. 1, Leu *et al*., 2015). Phase I (pre-bloom) occurs while solar irradiance is not sufficient for bloom development (predominantly net heterotrophy community), with limited interaction with pelagic and benthic realms. Phase II (bloom) begins in the spring once light available under the sea ice has passed a critical level where sea ice algae can grow exponentially (Gosselin *et al*., 1986; Mock & Gradinger, 1999; Hancke *et al*., 2018). This is the phase of highest ice algal productivity, however, interaction with the water column and benthos remains limited. Phase III (post-bloom) starts after ice temperature rises above a critical limit where melting and drainage of brine starts and is associated with a major loss of

in-ice communities. This leads to strong sympagic-pelagic-benthic coupling. The transparency of sea ice increases strongly during this phase due to snowmelt and melt pond formation together with a decrease in sea ice thickness, which typically induces pelagic phytoplankton blooms. The classic perception used to be that substantial pelagic production only takes off after the sea ice has retreated. However, this assumption has recently been challenged by observations of under-ice phytoplankton production from both advected (Johnsen *et al*., 2018) and local (Arrigo *et al*., 2012; Mundy *et al*., 2014; Assmy *et al*., 2017) blooms. During the ice-free period, stratification of surface waters caused by ice melt as well as riverine and glacial freshwater input often limits the supply of inorganic nutrients. Together with the extreme seasonal change in light availability, this results in a rather short and intense productive period in the high Arctic, which provides the entire annual biomass production for higher trophic levels (Sakshaug, 2004). Furthermore, many Arctic marine organisms have adapted their life cycles to the prevailing sea ice regime and take advantage of the highly concentrated sea ice algal food source prior to the phytoplankton bloom (Runge *et al.*, 1991; Søreide *et al.*, 2006; Søreide *et al.*, 2010; Daase *et al.*, 2013).

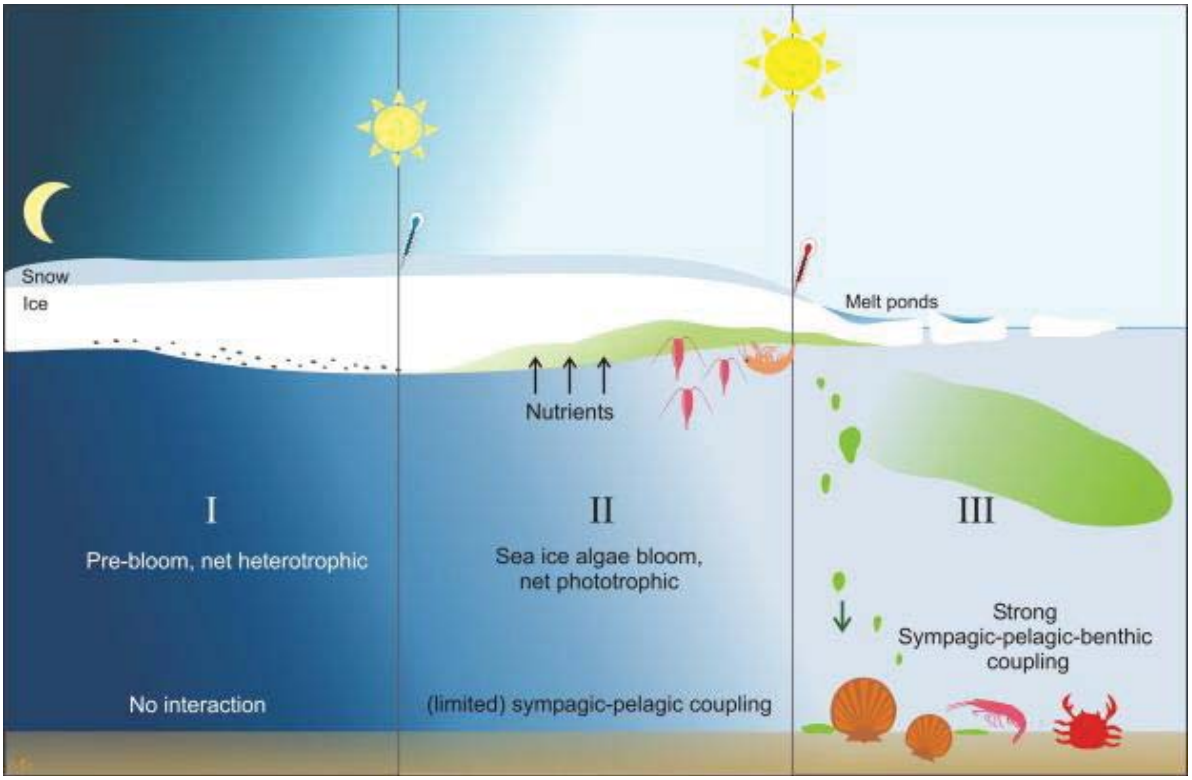

Fig. 1. Seasonal development of sympagic (sea ice algae) and pelagic algal blooms (Phase I – III) in ice-covered waters. Figure retrieved from Leu *et al.,* (2015).

A combination of physical and chemical factors of their environment ultimately controls the phenology and magnitude of sympagic and pelagic production in seasonally ice-covered waters; irradiance and nutrient availability are most important (Tremblay & Gagnon, 2009; Arrigo *et al.*, 2014a; Lewis *et al.*, 2018), but other drivers such as temperature and salinity also play an important role (Coello-Camba *et al.*, 2015; Petrou *et al*., 2011; Torstensson *et al.*, 2015). These physical factors vary greatly over time and space and influence physiology, abundance, biomass, and taxonomic composition of differently adapted species (Sakshaug, 2004; Litchman & Klausmeier, 2008). The extreme seasonal change in solar elevation at high latitudes is the dominant control of the Arctic light climate, but also the duration of sea ice cover, ice thickness, and snow depth are key parameters controlling the light regime in areas with seasonal or multiyear sea ice. Reported transmittance through ice and snow layers in the Arctic is often very low (between 0.023 – 9 % of incident irradiance; Leu *et al.*, 2010; Leu *et al.*, 2015; Campbell *et al.*, 2016; Assmy *et al.*, 2017; Hancke *et al.*, 2018). During the early phase of the bloom, when nutrients are plentiful, microalgal growth is thus often primarily limited by light (Leu *et al.*, 2015). Later, because of intense algal growth during bloom events, initially available inorganic nutrients become gradually depleted and develop into being the main limiting factor for further growth (Hansell *et al.*, 1993; Varela *et al.*, 2013; Danielson *et al.*, 2017). During this period algal communities might also be exposed to high levels of irradiance as snow and ice melt and the water column stratifies. Over the course of the bloom, microalgae populations can thus shift from a phase characterized by light-limited growth and accumulation to that of one or a combination of light limitation, nutrient limitation, photoinhibition, and in the case of sympagic algae, ice melt (Lavoie *et al.*, 2005; Galindo *et al.*, 2017; Mortenson *et al.*, 2017).

Changing Arctic

The Arctic is warming more rapidly than any other oceanic region on the planet. Rises in surface air temperatures are amplified over the Arctic ocean owing to positive feedbacks in the climate system (a phenomenon termed Arctic amplification). The most cited reason is the loss of sea ice cover (and thus also snow cover), which reduces the surface albedo; the lower the albedo, the more a surface absorbs heat, enhancing warming of the Arctic ocean (Screen & Simmonds, 2010). This have led to a rapid reduction in sea ice extent and thickness (Kwok *et al.*, 2009; Screen *et al.*, 2011), earlier melt onset (Nicolaus *et al.*, 2012), and declining snow cover (Screen & Simmonds, 2012). Since light climate in the Arctic is principally regulated by snow and ice cover (Mundy *et al.,* 2005; Aumack & Juhl, 2015), irradiance levels in surface waters are expected to increase. Stratification, which is an important factor in determining nutrient

availability (Tremblay *et al.*, 2015), is also expected to increase in a future Arctic. Progressive melting of sea ice, an increase in river discharge (due to increased precipitation and terrestrial ice melt), and glacial freshwater input all alter the density of the surface layer and consequently contribute to limiting the supply of nutrients from below the mixed layer to the photic zone (Peterson *et al.*, 2002). The Arctic Ocean is thus expected to shift from a predominantly light-controlled (ice-covered) to a more nutrient-controlled (open water) system (Carmack & Wassmann, 2006). Furthermore, atmospheric pCO_2 is rising, leading to elevated concentrations of CO_2 and lowered pH in seawater; a phenomenon commonly termed ocean acidification (OA; Caldeira & Wickett, 2003). OA is most pronounced in the Arctic because low temperatures increase CO_2 solubility, and low total alkalinity due to freshwater input and accumulation makes the system very sensitive to anthropogenic CO_2 loading (Yamamoto-Kawai *et al.*, 2009; AMAP, 2013). All these factors, i.e. irradiance, nutrient regimes, and pCO_2 levels are important in regulating microalgal ecophysiology. However, there is increasing evidence that changes in one environmental parameter affect the sensitivity to changes in others, so investigating synergistic and antagonistic interactions among multiple drivers are of major importance to make thorough predictions (Riebesell & Gattuso, 2015).

The resilience of microalgal assemblages towards environmental changes is determined by phenotypic plasticity of single individuals, functional diversity within a species, and species shift within a community (Collins *et al.*, 2013; Hoppe *et al.*, 2018a; Wolf *et al.*, 2018). Although physiological responses of microalgae species and communities have been investigated under various climate change scenarios, the results have been partly divergent, indicating large inter- and intraspecific differences in sensitivity towards changes in the environment. Hence, it is expected that progressing environmental change will strongly impact the timing of different types of algal blooms, their productivity, species composition, as well as food quality. The ongoing decrease in sea ice extent and thickness implies shorter bloom periods for ice algal production, but in return increases the potential for pelagic primary production both underneath the sea ice and in open water. Sea ice algae and phytoplankton blooms do not only differ with respect to timing but are also utilized by different groups of grazers. Hence, we can expect far-reaching consequences not only for the quantity and quality of annual algal primary production in the Arctic but also on downstream food webs. It is of particular importance in this context to understand how, and to what extent, sea ice-based vs. pelagic primary production will change with respect to timing and quantity. For developing realistic future scenarios, a proper

mechanistic understanding of the physiological and biochemical responses of sea ice algae and phytoplankton towards their changing environment is of key importance.

Photoacclimation and photoprotection

Photoacclimation describes the phenotypic response that occurs following changes in irradiance levels and represents many processes which serve to optimize cell activities such as photosynthesis, respiration, growth, and division (Falkowski & LaRoche, 1991; Brunet *et al*., 2011). In order to sustain functional photosynthesis under changing light conditions, microalgae utilize a wide range of acclimation mechanisms involving both short- and long-term physiological changes that allow cells to optimize photosynthesis while minimizing oxidative photodamage (Brunet *et al*., 2011). Short-term changes (minutes-hours) mainly concern an increase in non-photochemical quenching (NPQ) of excitation energy. This is mainly driven by the de- and re-epoxidation of available xanthophylls (e.g. diadinoxanthin and diatoxanthin, Fig. 2). These pigments can not only thermally dissipate excess excitation energy as heat, but the continuous chemical interconversion also consumes reductive energy and molecular oxygen (Falkowski & Raven, 2007; Lavaud & Goss, 2014) thereby decreasing the overall stress derived from electron pressure and the generation of reactive oxygen species (ROS). Furthermore, algae can decrease the transfer of excitation energy from pigment molecules to reaction centers by increasing intracellular self-shading (package effect) and by detaching antenna compounds from reaction centers (RC, Giovagnetti & Ruban, 2017). Long-term (hours-days) photoacclimation concerns changes of structure and composition of the photosystem and is characterized by changes in pigment composition (e.g. by increasing antioxidant carotenes and xanthophylls as well as decreasing light-harvesting pigments, Fig. 2), enzymatic activities involved in photosynthesis and respiration, cell volume, and chemical composition (Brunet *et al*., 2011).

Light in the natural environment is always variable, and a common strategy among algae is to acclimate to their average experienced growth environment (Behrenfeld *et al*., 2008), which is substantially lower than the experienced peak values. High light levels can thus have negative physiological effects in differently adapted species, resulting in high light stress and photoinhibition (Barlow *et al*., 1988; Galindo *et al*., 2017). Furthermore, it takes some time to adjust pigmentation for proper acclimation, hence, rapid increases in irradiance will remain a challenge (Kvernvik *et al*., under revision, Leu *et al*., 2006).

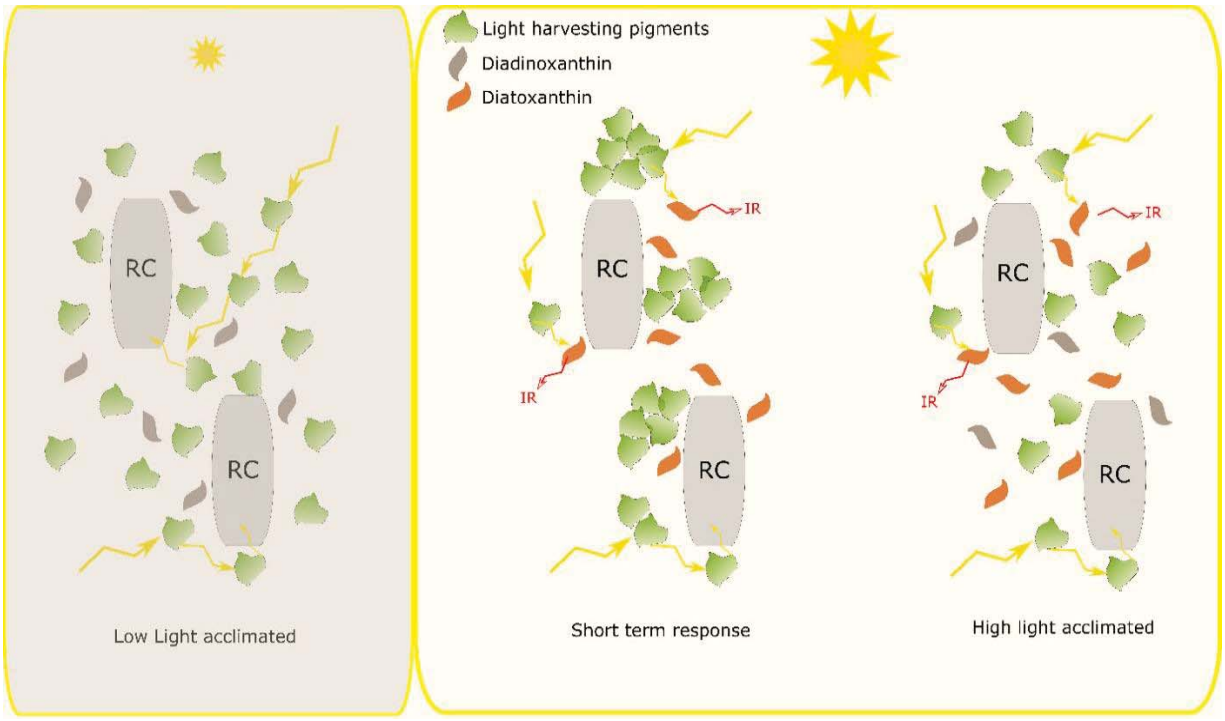

Fig. 2. Typical short- and long-term acclimation responses of microalgae. Short-term responses include structural re-arrangement of the light-harvesting antennae (e.g. pigment packaging) and increased non-photochemical quenching, driven by de-epoxidation of xanthophylls (e.g. diadinoxanthin and diatoxanthin). High light acclimated cells possess higher amount of xanthophylls, as well as decreased light-harvesting pigments compared to low light acclimated cells. RC designates reaction centers, and IR designates dissipation of excitation energy as infrared light (i.e. heat).

1.3 Objectives

The aim of this study was to investigate photophysiological and biochemical characteristics of sea ice algal and phytoplankton communities and identify their respective responses to changes in the environment. The overarching hypothesis of this thesis thus is:

Light availability is the dominant control of high Arctic microalgal communities. An increase in marine light climate due to a decreasing snow and sea ice cover will affect pelagic and sympagic algae differently, and sensitivity towards light stress will be modulated by interacting environmental variables.

Congruently, the main objectives of the individual research papers are as follows:

Paper I: To investigate physiological state and potential production of Arctic microalgae during the polar night and after re-illumination.

Paper II: To describe photophysiological and biochemical characteristics of natural sympagic vs. pelagic communities and investigate their respective responses towards changes in their abiotic environments; in particular, variations in irradiance and nutrient levels.

Paper III: To investigate potential responses to climate change in terms of increased light and ocean acidification in a common pelagic (*Thalassiosira hyalina*) vs. a sympagic (*Nitzschia frigida*) diatom.

1.4 Scope of thesis

Both natural microalgal communities and unialgal cultures were investigated in this thesis. Field observations combined with experimental studies (both *in situ* and laboratory experiments) were carried out to answer the research questions outlined in the section above. Microalgal responses to light availability are the unifying theme of the papers included in this thesis. In addition, **Paper II and III** investigates potential consequences of multiple stressors.

Paper I: In order to investigate potential for photosynthetic production of microalgae during the polar night, as well as their response to re-illumination, samples of natural phytoplankton communities were collected in January and December 2015. Experimental studies were conducted both *in situ* and in the laboratory. To assess the physiological state in which viable cells survive the polar night, photosynthetic activities were measured initially without exposing them to any light. Thereafter, the phytoplankton communities were exposed to different light levels and the temporal restoration of the photosynthetic apparatus upon re-illumination was studied.

Paper II: We carried out an extensive sampling campaign in Van Mijenfjorden during spring, 2017. The purpose of this study was to describe photophysiological and biochemical characteristics of natural pelagic and sympagic microalgal communities. To this end, photophysiological measurements were conducted on samples of pelagic and sympagic algae, collected from sea ice cores and open water in Van Mijenfjorden. At each sampling date and station, additional environmental data were obtained from vertical Conductivity, Temperature, and Pressure (CTD) profiles, autonomous observatories, and light measurements. Additional water and sea ice core samples were used to determine community composition, particulate organic carbon and nitrogen (POC/N), nutrient (NO_3, $SiOH_4$, and PO_4), and Chlorophyll (Chl) *a* concentrations (Knap *et al.,* 1996). To strengthen the validity of the field observations, we carried out a short (24 h) *in situ* experiment, comparing carbon fixation of pelagic and sympagic algal assemblages under a range of irradiance levels.

Paper III: As a supplement to the field study (**Paper II**), we carried out a laboratory experiment comparing the common Arctic diatoms *Thalassiosira hyalina* (pelagic) and *Nitzschia frigida* (sympagic**, Paper III**). We investigated the effects of light stress (shift from 20 to 380 µmol photons m^{-2} s^{-1}) under contemporary and future pCO_2 (400 vs. 1000 µatm), to determine these species´ performance in a changing Arctic. Here we followed the phenomenological and physiological reactions as well as the accompanying gene expression patterns.

Chapter 2

Approach

2.1 Study area

Spitsbergen is located between 76° N and 80° N and is the largest island of the Svalbard archipelago (Norway). The sea ice conditions around Spitsbergen vary according to season, degree of exposure to storm and waves, and the oceanic circulation around the archipelago (Alexeev *et al.,* 2017). The West Spitsbergen Current transport warm (> 3 °C) and saline (> 34.9) Atlantic Water into the Arctic Ocean, and thus serves as a heat source for the region (Swift & Aagaard, 1981). The west coast of Spitsbergen is characterized by several fjord systems with altering inflow of different water masses. While some fjords, such as Isfjorden, are open fjord systems and directly influenced by the warm Atlantic Water (Berge *et al.*, 2005; Nilsen *et al.*, 2008), Van Mijenfjorden offers favorable conditions for studying sea ice. Van Mijenfjorden, the second largest fjord in western Svalbard, is 50 km long and ~10 km broad. The mouth of the fjord is largely closed off by the island Akseløya, which together with a shallow sill limits the exchange of fjord water with the warm Atlantic Water. Furthermore, a rather closed fjord is less exposed to winds and waves, which offers favorable conditions for a stable sea ice cover. Time for freeze-up in this fjord usually covers a wide time span ranging from November to January, while the ice normally breaks up between June and July depending on ice coverage and thickness (Høyland, 2009). Because of increased winter temperatures in Svalbard, however, the period of ice coverage in Van Mijenfjorden has become shorter during the latest years (Osuch & Wawrzyniak, 2017). Arctic fjords are therefore well suited for investigating both sympagic and pelagic microalgal communities and identifying their responses towards changes in the environment.

2.2 Methods

Different methods were used to identify and explore ecophysiological responses of Arctic microalgae; (i) variable fluorescence characteristics by fast repetition rate fluorometer (**Paper I, II and III**), (ii) ^{14}C-based net primary production (**Paper I and II**), (iii) pigment composition (**Paper II and III**), and (iv) gene expression patterns (**Paper III**). By this, we addressed the functionality of the photosynthetic apparatus regarding the light-dependent reactions, the ability of the algae to fix carbon, as well as the underlying mechanisms that determined these responses. Gene expression patterns were covered by a collaborator and are therefore not presented as detailed within this thesis.

Photophysiology by fast repetition rate fluorometry

Chl *a* variable fluorescence measurements is a rapid, non-invasive and sensitive procedure for monitoring photosynthetic performance of algae (Oxborough, 2012), and describes the phenomenon where light absorbed by Chl *a* molecules at one wavelength is re-emitted at another (longer) wavelength (fluorescence; Johnsen & Sakshaug, 2007). Once a photosystem II (PSII) reaction center captures a photon an excited state of a Chl *a* molecule is formed and there are several possible de-excitation pathways; (i) re-emission of light as fluorescence, (ii) kinetic transfer and dissipation of energy to the environment in the form of heat, and (iii) photochemistry which eventually lead to the synthesis of high-energy molecules i.e. ATP and NADPH. Excitation energy can also be transferred to O_2 and create damaging and reactive oxygen species (Müller et al. 2001). By measuring the fraction of absorbed light that is re-emitted as fluorescence, we can thus examine the light-dependent rates of photosynthetic electron transport in algae.

Chl *a* variable fluorescence measurements were measured on natural microalgal assemblages (**Paper I and II**) and on diatom cultures (**Paper III**) using Fast Repetition Rate (FRR) fluorometers. The FRR technique applies a sequence of saturating excitation pulses at microsecond intervals to induce fluorescence transients. In addition to initial (F_0) and maximum (F_m) fluorescence, the FRR technique allows for determination of the absorption cross section of PSII (σ_{PSII}) and the rate of reopening of reaction centers (τ_{ES}) from one single photochemical turnover of PSII (Fig. 3a, Kolber *et al*., 1998). Photosynthetic rates are related to irradiance in a non-linear fashion (Fig.3b) and photosynthesis vs. irradiance (PE) curves can provide information on the photoacclimative state of microalgae at the moment of sampling. At the lowest irradiances, photosynthetic rates increase linearly with irradiance at a rate (α) proportional to the light utilization capacity of the measured sample. As irradiance increases,

photosynthetic rates reach saturation (i.e. the maximum photosynthetic rate, ETR_{max}), that reflects electron transport capacities downstream of PSII. The ratio of ETR_{max} to α is referred to as the light saturation index, E_k, which indicate the saturation irradiance and the photoacclimative state of the algae (Fig. 3b, Sakshaug *et al.*, 1997). To record photosynthesis versus irradiance (PE) curves in **Paper I, II and III**, the FRR fluorometer provided 10 x 3 min levels of white Photosynthetically Active Radiation (PAR) ranging from 0 – 2000 µmol photons m^{-2} s^{-1} depending on acclimation status of the microalgae measured. Following actinic light periods minimum (F_0') and maximum (F_m') fluorescence in light acclimated cells were determined. Parameters derived from Chl *a* variable fluorescence measurements used in **Paper I, II and III** are described in Box 1.

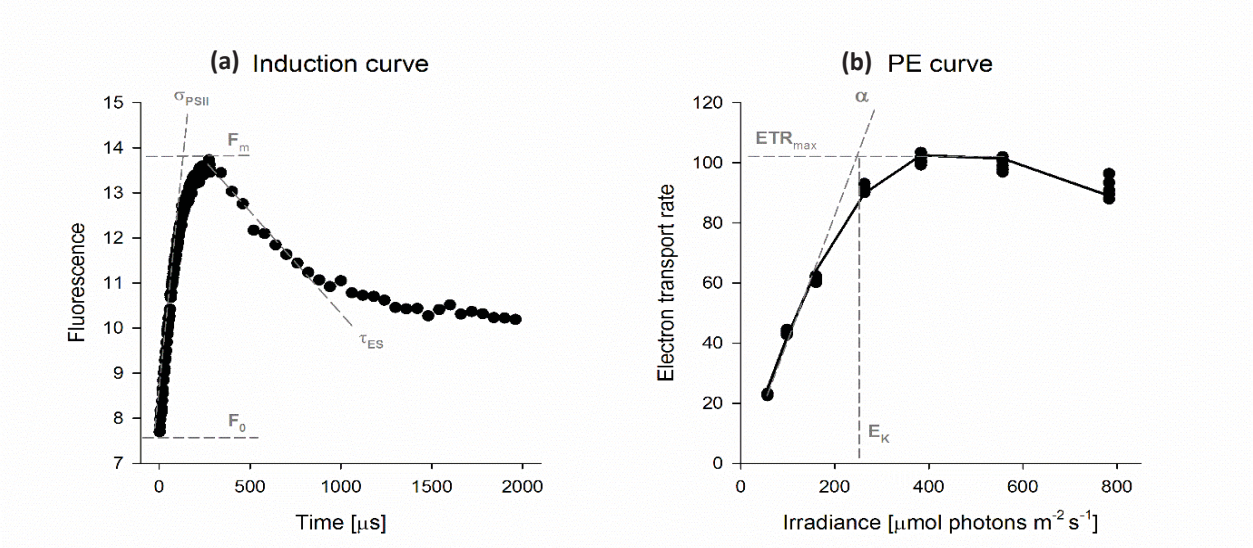

Fig. 3. Chlorophyll (Chl) *a* variable fluorescence parameters derived from (**a**) one single photochemical turnover of PSII and (**b**) photosynthesis vs. irradiance (PE) curve. Data retrieved from high light acclimated *Thalassiosira hyalina* cells grown under 400 µatm (**Paper III**).

Box 1. *Chl a variable fluorescence parameters*

Maximum quantum yield of PSII (F_v/F_m), commonly used to assess health status of algae (Sakshaug *et al*., 1997), was calculated according to Krause & Weis, 1991:

$$\frac{F_m - F_0}{F_m}$$

σ_{PSII} (nm^2 PSII^{-1}) designates the absorption cross-section of PSII light-harvesting antenna (i.e., the energy delivery), while τ_{ES} (ms) is the rate of reopening of PSII reaction centers, and thus serves as a proxy of the rate the plastoquinone (PQ) pool manages to move electrons away from PSII.

Non-photochemical quenching of Chl *a* fluorescence reflects the ability of a cell to dissipate excess energy as heat (Sakshaug *et al*., 1997). In **Paper I** it was quantified through the parameter NPQ (Bilger & Björkman, 1990):

$$\frac{F_m - F'_m}{F'_m} \cdot E_{PAR}$$

In **Paper II and III**, Normalized Stern Volmer coefficient was used to assess non-photochemical quenching (Oxborough, 2012):

$$\frac{F'_q}{F'_v} - 1 = \frac{F'_0}{F'_v}$$

Following actinic light exposure, electron transport rate through PSII (ETR) was calculated as:

$$\frac{F'_m - F'_0}{F'_m} \cdot E_{PAR}$$

The calculated ETR was plotted against actinic irradiance to generate photosynthesis versus irradiance curves (PE curves), from which the light utilization coefficient (α) and the maximum photosynthetic rate (ETR_{max}) were derived using the model fit of Eilers and Peeters (1988).

The light saturation index (E_k [µmol photons m^{-2} s^{-1}]) was then calculated as ETR_{max}/α.

^{14}C-based net primary production

Photosynthetic characteristics based on fluorescence measurements do not necessarily directly translate into primary production (Schuback *et al*., 2017). As described above, Chl *a* variable fluorescence can be used to assess the light-dependent rates of photosynthetic electron transport through PSII, while carbon fixation includes the dark reaction of photosynthesis. If photosynthesis is measured as carbon fixation, the term net primary production (NPP) represents the carbon fixation rate following all daytime and night-time respiratory losses and is subsequently available to the next trophic level (Sakshaug *et al*., 1997). By combining fluorescence measurements and carbon fixation we can thus gain important knowledge on how efficiently photosynthetic electron transport is translated into biomass accumulation. In **Paper I**, ^{14}C-based NPP was measured, both, *in situ* and in the laboratory. *In situ* measurements were carried out on natural pelagic algal assemblages moored for 24 h at 0.3 m below the sea surface in Kongsfjorden. In the laboratory, ^{14}C-uptake measurements were made before and after natural algal assemblages were incubated at different irradiance levels. In **Paper II**, *in situ* ^{14}C-based NPP measurements were carried out on samples of natural pelagic and sympagic algal assemblages moored for 24 h underneath the sea ice in van Mijenfjorden. Here, experimental bottles with different optical coating (0 – 100 % transmission) were used to record and compare ^{14}C-based PE curves between sympagic and pelagic algae. For all NPP measurements, samples were amended with $NaH^{14}CO_3$, and beta radiation was measured with a liquid scintillation counter. Parameters derived from ^{14}C-based carbon fixation used in **Paper I and II** are described in Box 2.

Box 2. ^{14}*C-based net primary production parameters*

^{14}C-based fixation rates in **Paper I and II**, were measured over a period of 24 h, and thus represent net primary production rates of microalgae.

^{14}C fixation rates (µg C (µg Chl *a*)$^{-1}$ d^{-1}) were calculated according to Hoppe *et al*., (2015):

$$NPP = \frac{[DIC] \cdot DPM_{sample} \cdot 1.05}{DPM_{100\%} \cdot t \cdot [Chl]}$$

[DIC] and [Chl] denote concentrations of dissolved organic carbon (DIC) and chlorophyll a (Chl) in the sample. DPM_{sample} is the disintegrations per min (DPM), while $DPM_{100\%}$ denotes the total count added to the samples. *t* (time) denotes the duration of the incubation in days, and the number 1.05 is the uptake discrimination factor.

In **paper II**, calculated ^{14}C fixation rates were plotted against actinic irradiance to generate ^{14}C-based PE curves, from which fit parameters (P_{max}, α and E_k) were derived using the model fit of Eilers & Peeters (1988):

- ^{14}C-derived P_{max} is the light saturated maximum rate of ^{14}C uptake (µg C (µg Chl *a*)$^{-1}$ d^{-1}).
- ^{14}C-derived α is the light-dependent increase in the rate of ^{14}C-uptake before saturation (µg C (µg Chl *a*)$^{-1}$ d^{-1} (µmol photons m^{-2} s^{-1}).
- ^{14}C-derived E_k is the light saturation parameter (µmol photons m^{-2} s^{-1}).

Pigment composition and biochemical characteristics

Light utilization is determined by the pigment suite in the particular algae (Roy *et al*., 2011). Photosynthetic pigments are molecules that are specialized in absorbing light in the visible part of the spectrum (400 – 700 nm) called photosynthetic active radiation (PAR). Pigments can be separated into two functional groups; (i) light-harvesting or (ii) photoprotective pigments. Light-harvesting pigments absorb light and transfer the energy to PSII, thereby contributing to photosynthesis. The main function of photoprotective pigments, however, is to convert the absorbed light into heat to prevent photodamage (Roy *et al*., 2011). In response to low and high light, algae can alter the fraction of light-harvesting and photoprotective pigment content (Brunet *et al*., 2011). Identifying and quantifying algal pigments can thus provide considerable information on photophysiological state of algae. Determination of pigment composition by means of high-performance liquid chromatography (HPLC) is a widely used method to gain information on algal community and photoacclimation status (Higgins *et al.,* 2011) and was used to assess natural communities of sympagic and pelagic algae in **Paper II**, as well as unialgal cultures in **Paper III**. Identification of pigments was based on retention times, pigment spectra obtained with diode array OD detector, and commercially available pigment standards. Different pigment groups were used to assess the light-harvesting (e.g. Chl *a*, fucoxanthin and Chl c1, c2 and c3) as well as the photoprotective (diadinoxanthin and diatoxanthin, DD+DT) capacity of pelagic and sympagic algae.

Changing environmental conditions can cause alterations in the proportions of the major elements carbon (C) and nitrogen (N) in algal cells. Both irradiance and NO_3 are known to exert strong control on C:N ratios (Gosselin *et al*., 1990): C:N ratios may increase as a result of acclimation to high irradiances (i.e. a relative increase in cellular C quota because excess light energy is drained in carbon fixation) or nutrient limitation (i.e. a relative decrease in cellular N quota). Measurements of stoichimetric ratios in algae are therefore widely used to assess carbon production (**Paper II and III**), nutrient-based productivity (C:N ratios, **Paper II**), as well as nutritional quality.

Chapter 3

Main findings

In the following chapter, a general overview is given of the main findings of field observations and experimental studies, which have been presented in the three research articles. A detailed presentation of the actual data can be found in the respective papers.

3.1 Irradiance regimes in the high Arctic: Polar night, under ice, and open water

The Arctic is characterized by extreme fluctuations in light intensity. At the study sites in this thesis (~78° N), the sun does not rise above the horizon from the end of October to mid-February, resulting in very low ambient light levels in winter, which is far below the detection limits of conventional irradiance sensors (**Paper I**, Fig. 4). Following the return of the sun in early spring, solar elevation increases rapidly, and from approximately mid-April the midnight sun period starts and lasts until end of August. In this period, marine irradiance levels can fluctuate highly due to the variability of ice- and snow-cover, rapid shifts in cloud cover, and later in the season, sediment loading as a result of temperature increase coupled with riverine and glacial freshwater input (**Paper II**, Fig. 4).

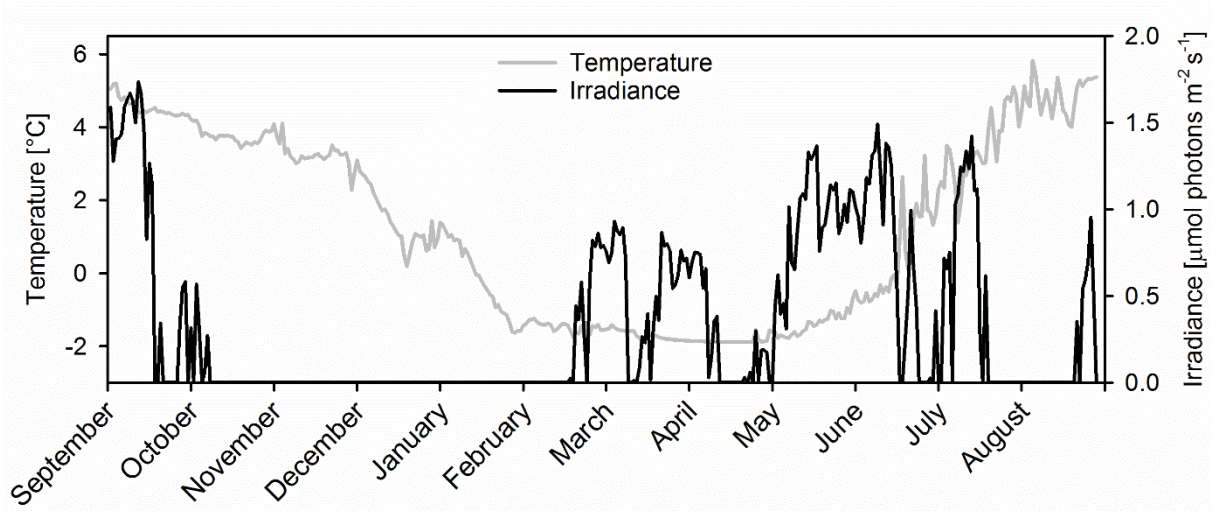

Fig. 4. Temporal development of temperature (°C) and irradiance (µmol photons m^{-2} s^{-1}) at station Vmf 1 in Van Mijenfjorden (~78°N, **Paper II**). At the study site, the sun did not rise above the horizon from the 27th of October to the16th of February (polar night). Data retrieved from multi-parameter ocean observatory established at 12 m depth in 2017 (**Paper II**).

Irradiance regimes experienced by pelagic and sympagic algae can be very different. Transmittance through ice and snow layers during spring (2017) in Van Mijenfjorden was lower (between 0.5 - 26 % transmittance of incoming irradiance) than in surface layers of open water (ranging between 49 – 92 % of incoming irradiance, **Paper II**). Sea ice algal assemblages live in a spatially confined environment that is not normally undergoing rapid change, and therefore usually experience gradually changing irradiances on low amplitudes (Pa**per II,** Fig. 5). On the contrary, pelagic phytoplankton could experience fluctuations in light intensity with high frequency (minutes), coupled with high amplitudes (from darkness to full sunlight) due to vertical mixing of cells within deeply mixed layers (**Paper II**, Fig. 5). For example, pelagic algae in Van Mijenfjorden on the 21st of April 2017 could experience irradiance levels ranging between 0 and 100 µmol photons m^{-2} s^{-1}, due to vertical movement within a mixed layer depth of 20 m. In comparison, irradiance levels at the ice-water interface the same day ranged between 0.1 and 0.8 µmol photons m^{-2} s^{-1}. Furthermore, fluctuations due to weather conditions are most extreme in the high light range, so the effect of cloud cover from day-to-day was less important at the ice-water interface than in the uppermost part of the water column (Fig. 5).

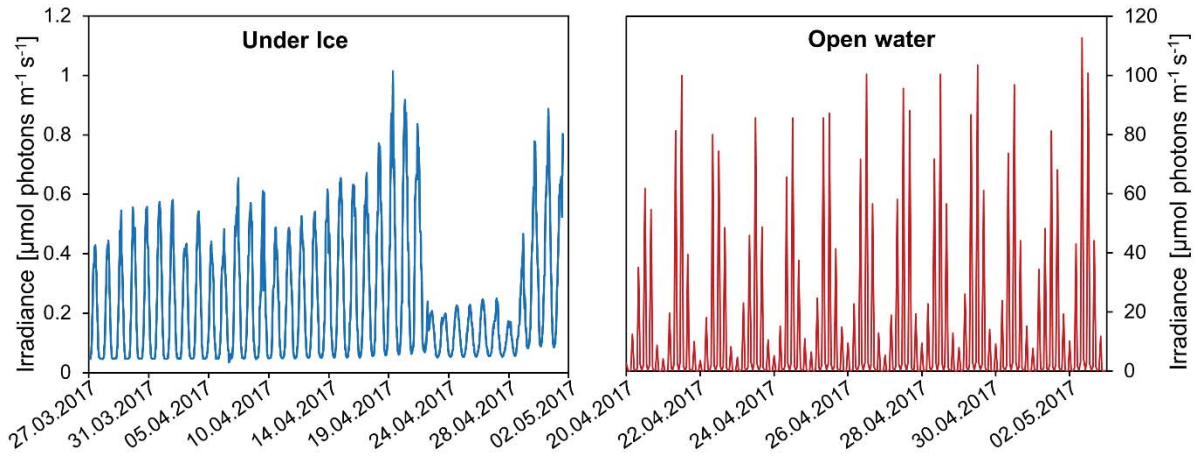

Fig. 5: Exemplary temporal changes of irradiance regimes at the ice-water interface (blue) and in open water (red). Daily fluctuations of irradiance regimes in open water were modeled with a mixing pattern down to 20 m. Data retrieved from **Paper II**.

3.2 Photophysiological characteristics of Arctic microalgae

In both pelagic and sympagic algae, responses towards variations in irradiance were stronger and more dynamic than the response towards changing NO_3 and pCO_2 levels. Hence the focus of this thesis is on how irradiance levels affect different aspects of microalgal physiology. Both the pelagic and sympagic ecosystems hosted diverse but distinct microalgal communities. We observed some similarities between the responses of pelagic and sympagic algae to increasing irradiance, such as an increase of photoprotective efforts (i.e. *de novo* synthesis of DD+DT and increased NPQ). However, the results also revealed that responses towards the highest irradiances differed markedly between pelagic and sympagic algae, as the latter exhibited much higher sensitivity.

Community composition

Phytoplankton communities that were analyzed during the polar night (i.e. in December and January 2015) were sampled with plankton nets (20 μm mesh size), and thus represent only the largest size fraction of the community present in winter (**Paper I**). We found diverse and active phytoplankton communities during the polar night at 78°N, which consisted of both autotrophic and heterotrophic species. The most abundant taxa were centric diatoms of *Thalassiosira* sp., dinoflagellates of *Gymnodinium* sp. as well as heterotrophic ciliates belonging to the family Tintinnida (**Paper I**). In Van Mijenfjorden (2017) in April and May (under ice sampling), three major groups were found to dominate the phytoplankton community: diatoms, dinoflagellates and prymnesiophyceae (**Paper II**). Particularly abundant taxa were the centric diatoms *Chaetoceros* sp. and *Thalassiosira* sp., the pennate diatom *Fragilariopsis* sp. and the colony-forming haptophyte *Phaeocystis pouchetii*. In June (sampling in open waters), surface layers were largely dominated by one known brackish and mixotrophic genus; *Olisthodiscus* sp. (48 % of total abundance), while the deeper depths were dominated by >80 % *Phaeocystis pouchetii.* In August (sampling in open waters), heterotrophic and mixotrophic cryptophytes and dinoflagellates dominated the pelagic protist assemblage (**Paper II**). Hence, the pelagic community was in most instances very heterogenous, but also highly variable depending on time of year, depth and station. In comparison, sea ice algal assemblages were much more homogenous. Here, pennate diatoms mainly dominated the algal assemblage across all stations and throughout the sampling period (between 37 – 99 % of total cell abundances, **Paper II**). Furthermore, the community was also functionally distinct from the pelagic assemblage, as the most abundant taxa within sea ice were *Nitzschia* sp., *Navicula* sp. and *Fragilariopsis* sp.

Winter is coming: How do phytoplankton spend the polar night?

In order to assess the physiological state of phytoplankton communities sampled during the polar night, they were measured without exposing them to light (**Paper I**). F_v/F_m, the maximum dark-acclimated PSII quantum yield, ranged between 0.08 and 0.39 during the polar night, showing that initially some algae were not in a completely unhealthy photosynthetic state. Upon re-illumination, we observed strong and rapid changes (≤20 min) in σ_{PSII} ($p = 0.002$) and τ_{ES} ($p = 0.001$), i.e. the energy delivery to PSII and the reopening of PSII reaction centers respectively. Hence, Arctic pelagic algae were able to immediately utilize available energy for photosynthesis, and increase photosynthetic efficiency as indicated by a rise in F_v/F_m shortly after re-illumination. After only 24 h in constant low light (1 µmol photons m^{-2} s^{-1}), values approached an average yield of 0.49 ± 0.03, which is in the range of the highest values observed in phytoplankton communities during early spring in Van Mijenfjorden (**Paper II)**. High photosynthetic capacity and NPP were also established after 24 h of re-illumination. ETR_{max}, which reflects electron transport capacities downstream of PSII, reached maximum values after just 24 h of re-illumination (**Paper I**). Also, there was no observed difference in carbon uptake at 6.5 µmol photons m^{-2} s^{-1} between cells kept in darkness or 6.5 µmol photons m^{-2} s^{-1} for 2 days prior to NPP measurements. No apparent carbon fixation was however observed in algae incubated for 24 h near the surface during *in situ* polar night conditions (**Paper I**).

The transition to permanent light exposure: How do photophysiological responses differ between sympagic and pelagic algae?

In Van Mijenfjorden, we followed photophysiological and biochemical characteristics of natural sympagic and pelagic microalgal communities from the 9th of March to the 23rd of August 2017 (**Paper II**). Bottom ice Chl *a* concentrations peaked (~300 mg L^{-1}) between the 7th of April and the 2nd of May; surprisingly this occurred at the same time as pelagic Chl *a* concentrations which approached ~16 mg L^{-1} between the 23rd of April and the 2nd of May. The accumulation of algal biomass resulted in a rapid drawdown of open water NO_3. In sea ice however, NO_3 levels varied to a great extent between dates and stations and were dependent on snow cover; NO_3 levels were significantly lower under low compared to high snow cover. In order to compare ecophysiological responses of natural pelagic and sympagic algae assemblages, we followed variable fluorescence characteristics, carbon fixation rates, stoichiometry, and pigment composition of the two communities in Van Mijenfjorden (**Paper II).** Throughout the sampling period, snow cover on sea ice was rather variable due to wind drift and melting processes later in the season. Furthermore, in June and August, open water stations were influenced by meltwater and sediment loading. These dynamics resulted in highly

variable under-ice and open water irradiances (**Paper II**). To estimate the light climate for each sample, we derived the irradiance levels as the average of 24 h before the sample was taken. Generally, pelagic phytoplankton communities showed absent (e.g. in F_v/F_m and FRRf-derived α) or rather subtle (e.g. in the FRRf-derived ETR_{max} which showed a slightly positive relationship with irradiance) trends with increasing irradiance. Physiological parameters related to the PSII antenna structure, specifically the functional absorption cross-section (σ_{PSII}) and photosynthetic yield (F_v/F_m), did vary as a result of taxonomic differences within the pelagic community. For example, F_v/F_m remained in the range between 0.32 – 0.55 in communities dominated by diatom species, between 0.24 – 0.41 in communities dominated by *Phaeocystis pouchetii*, while the lowest values (between 0.06 – 0.35) were measured in communities dominated by mixotrophic and heterotrophic species (**Paper II**). In contrast to the subtle trends in the pelagic community, the sympagic assemblage reacted more strongly towards increasing irradiances: Photosynthetic efficiency (F_v/F_m, $p = 0.0006$) and capacity (ETR_{max}, $p = 0.04$) only increased with irradiance in the low average irradiance range between 0 - 8 µmol photons m^{-2} s^{-1}, and thereafter decreased rapidly with further increases in irradiance levels (Fig. 6a, **Paper II**). The *in situ* incubation experiment conducted underneath the sea ice in Van Mijenfjorden also revealed striking differences between the sympagic and pelagic algal assemblages (**Paper II**). Results from the FRRf-based PE curves showed that the ETR_{max} was higher in pelagic than sympagic algae ($p < 0.001$), while α remained similar, resulting in significantly higher FRRf-derived E_k in pelagic algae ($p = 0.02$, Fig. 6b). After 24 h incubation underneath the sea ice, pelagic algae showed higher carbon fixation rates at all irradiances compared to the sympagic algae (Fig. 6c), resulting in a higher ^{14}C-derived α in pelagic (0.009 µg C (µg Chl *a*)$^{-1}$ d^{-1} [µmol quanta $m^{-2}s^{-1}]^{-1}$) compared to sympagic (0.004 µg C (µg Chl *a*)$^{-1}$ d^{-1} [µmol quanta $m^{-2}s^{-1}]^{-1}$) algae. Furthermore, as pelagic algae did not show any light saturation during the ^{14}C based PE curve, sympagic algae had a light saturation parameter for photosynthesis (^{14}C-derived E_k) of 43 µmol photons m^{-2} s^{-1} (Fig. 6c, **Paper II**).

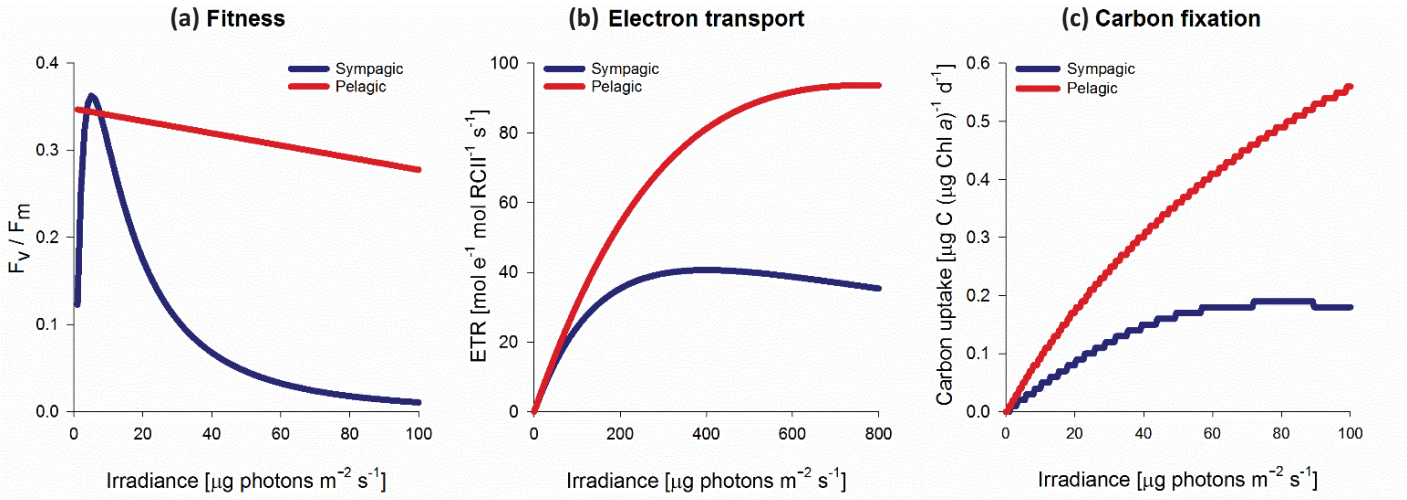

Fig. 6. Modelled relationships from **Paper II**; (a) changes of F_v/F_m with increasing irradiances, (b) FRRf-derived photosynthesis vs. irradiance (PE) curves and (c) ^{14}C based PE curves in pelagic (red) and sympagic (blue) algal assemblages.

Thalassiosira sp. was among the most abundant taxa in the pelagic community, both during the polar night (**Paper I**) and in early spring (**Paper II**). Within sea ice however, pennate diatoms belonging to the genus *Nitzschia* sp. largely dominated the algal assemblage (**Paper II**). In **Paper III**, we investigated the effects of light stress (shift from 20 to 380 µmol photons m^{-2} s^{-1}, resembling upwelling or ice break-up events) under contemporary and future pCO_2 levels (400 vs. 1000 µatm) in *Thalassiosira hyalina* and *Nitzschia frigida*. High light induced some similar photophysiological responses in both species; however, *N. frigida* reacted both more quickly and more strongly than *T. hyalina* (**Paper III**). In the short-term (first 12 h), high light exposure caused the maximum dark-acclimated PSII quantum yield (F_v/F_m) to gradually decrease in *T. hyalina* (p = < 0.001), while in *N. frigida* the same extent of reduction was observed after only 15 min (p = < 0.001, Fig. 7). Also, NPQ increased gradually in *T. hyalina* and reached maximum values between 12 h and 24 h (p = < 0.001). *N. frigida*, in comparison, reached highest NPQ levels after just 3 h (p = 0.003). During the intermediate response to high light exposure (between 24 – 72 h), both species increased their photoprotective pigment quotas (DD+DT) and decreased their light-harvesting pigment content (however this was only evident when normalizing to POC content in *T. hyalina,* **Paper III**). After 24 hours the pelagic diatom had successfully acclimated to the high light; F_v/F_m increased (Fig. 7), coupled with decreasing NPQ. Electron transport rates (ETR) at the applied irradiance level increased and eventually exceeded the initial rates in low light.

The successful acclimation of *T. hyalina* eventually manifested in significantly higher growth rates ($p = 0.041$) and POC production ($P = 0.006$) in high light acclimated cells compared to low light acclimated cells (Fig. 7, **Paper III**). Contrary to the observations from the pelagic diatom, the sea ice diatom *N. frigida* did not show any clear indications of recovery of the photosynthetic parameter F_v/F_m. Rather, this variable remained at a level similar to that measured after 15 min of HL exposure (Fig. 7, **Paper III**). Also, ETR remained at similar levels to the initial measurements taken in low light. The unsuccessful acclimation of *N. frigida* resulted in significantly reduced growth rates under high light compared to low light ($P < 0.001$), whilst POC cellular production remained statistically similar (Fig. 7, **Paper III**).

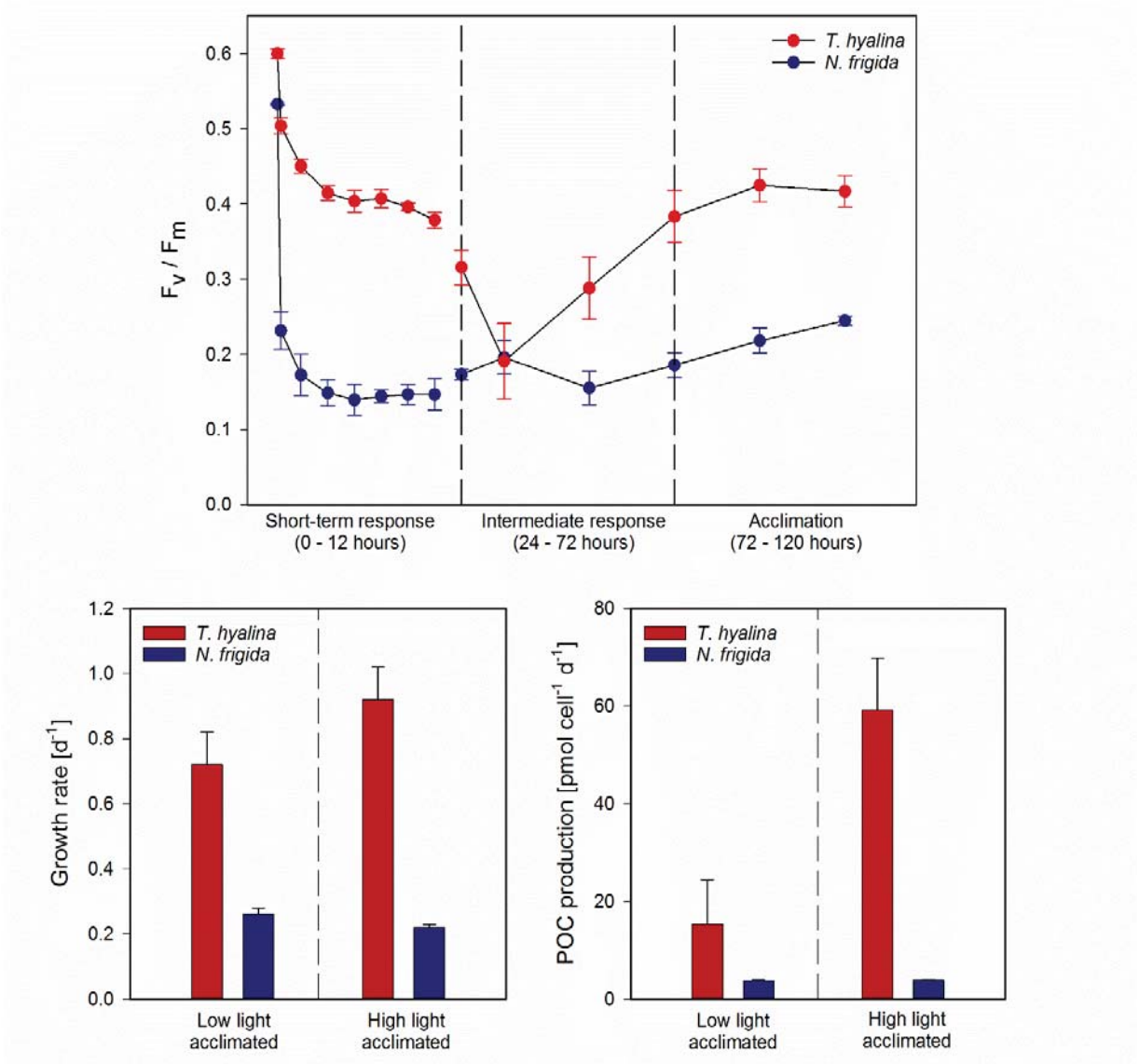

Fig. 7: Temporal changes of F_v/F_m in *Thalassiosira hyalina* (red) and *Nitzschia frigida* (blue) in response to high-light exposure under contemporary pCO_2 levels (400 µatm). Reponses are divided into; short-term response (0 - 12 hours); intermediate response (24-72 h), and; acclimation (72 – 120 h). The two bottom graphs show growth rate µ (d^{-1}) and POC production (pmol $cell^{-1}$ d^{-1}) in low light and high light acclimated *T. hyalina* (red) and *N. frigida* (blue) cells. Data retrieved from **Paper III**.

3.3 Combined stressors: Potential modulations of light-induced responses

In order to assess how responses towards variations in irradiance could be modulated by other environmental variables, we studied interactive effects between irradiance and NO_3 levels in natural pelagic and sympagic assemblages in Van Mijenfjorden (**Paper II**), as well as how responses to high light were affected by high pCO_2 in two common Arctic diatoms (*T. hyalina* and *N. frigida,* **Paper III**).

In natural pelagic assemblages, no notable trends in physiological or biochemical parameters were observed with decreasing NO_3 levels. Similarly, to the higher sensitivity towards high light stress, sympagic algae were also more responsive to variations in NO_3 levels. Synergistic effects between irradiance and NO_3 levels were evident in natural sympagic algal assemblages: Under the highest light, concurrent nutrient limitation contributed to the strongly reduced photosynthetic efficiency (F_v/F_m, $p = 0.0008$; **Paper II**).

In **Paper III** we assessed how a pelagic (*T. hyalina*) and sympagic (*N. frigida*) diatom responded to ocean acidification, by comparing photophysiological characteristics from low and high light acclimated cells under low (400 µatm) and high (1000 µatm) pCO_2 levels. Under low light conditions, *T. hyalina* generally did not respond to increased pCO_2 levels, as we did not observe any difference in photophysiological parameters between low and high pCO_2. *N. frigida*, however, responded to OA under low light: F_v/F_m ($p = 0.005$) and α ($p < 0.001$) were significantly reduced, in line with a slightly decreased POC production under high vs. low pCO_2 levels ($p = 0.030$, **Paper III**). In both *T. hyalina* and *N. frigida,* high *p*CO2 affected light responses under high light (**Paper III**). In *T. hyalina*, F_v/F_m values were significantly lower under 1000 µatm compared to 400 µatm ($p = 0.009$), while NPQ ($p = 0.004$) and DD+DT quotas ($p < 0.001$) were significantly higher under OA. This translated into reduced growth rates under high compared to low pCO_2 levels under high light conditions ($p = 0.004$). Similarly, *N. frigida* cells were also more negatively affected by high light under OA. For instance, growth rates, as well as POC and PON production responded negatively to high light, but under OA, the difference between low and high light treatments were larger, and the responses therefore more intense (**Paper III**).

Chapter 4

Discussion

At the study sites in this thesis (~78°N), the sun stays above the horizon for approximately four months (polar day), and below the horizon for four months (polar night). The resulting extreme seasonal change in light availability is the dominant control of the high Arctic ecosystem. Here we show that pelagic phytoplankton maintained the photosynthetic machinery during the polar night (**Paper I**), effectively exploited very low irradiances (**Paper I and II**), handled photophysiological stress well (**Paper II and III**), and exhibited high photoacclimative capacity towards increasing irradiances (**Paper II and III**). In comparison, the ability of sympagic algal assemblages to take advantage of increases in irradiance was restricted to rather low irradiance ranges (**Paper II**), and they exhibited higher sensitivity towards high light stress (**Paper II and III**).

4.1 Bloom initiation – From no light to low light

The polar night was once thought to be void of biological activity. Recent research, however, challenges this assumption by presenting higher biological activity and diversity on virtually all trophic levels than previously thought, including chloroplast-bearing microbes, such as diatoms and flagellates (**Paper I**, Berge *et al*., 2015a, 2015b, Vader *et al*., 2014). The winter and early spring are particularly critical for the development of the spring phytoplankton bloom because the viable overwintering seed population directly determines bloom initialization. During the polar night, we found diverse and viable forms of autotrophic species, including *Thalassiosira* sp. (**Paper I**). *Thalassiosira* sp. are key phototrophs in the Arctic, commonly blooming during the spring in Svalbard fjords (**Paper II**, Von Quillfeldt, 2005). Physiological characteristics of these algae assemblages indicated that Arctic autotrophs were able to maintain an active photosynthetic apparatus during the polar night, even though the ambient light was not sufficient to support any measurable NPP. This ensured a fast recovery and utilization of even very low constant irradiances (1 µmol photons m^{-2} s^{-1}) upon re-illumination (**Paper I**). After only 24 h of re-illumination, the phytoplankton assemblages displayed similar photosynthetic efficiency and capacity (i.e. F_v/F_m and ETR_{max}) as pelagic communities blooming in nutrient-replete waters in early spring in Van Mijenfjorden (**Paper II**). Furthermore, measurable rates of NPP at light levels as low as 0.5 µmol photons m^{-2} s^{-1} indicated that phytoplankton communities can remain net productive under more extreme low

light conditions than previously thought (**Paper I**). Due to the strong seasonality in the Arctic, the periods of favorable light conditions for carbon fixation and growth are short, so it seems likely that exploiting very low irradiances would be advantageous for Arctic algae, especially in early spring. In fact, beneath the sea ice in Van Mijenfjorden between 23rd of April and 2nd of May, we observed a peak in pelagic Chl *a* concentrations (**Paper II**). Irradiance levels in the water column underneath the sea ice at that point were very low, both due to absorption by sympagic algae (which reached peak Chl *a* values at the same time) and water. Photophysiological measurements confirmed that the under-ice phytoplankton assemblage was in a healthy condition and able to photosynthesize at these very low irradiances (**Paper II**). This is in line with various studies that have suggested specific adaptions of polar microalgae to be able to grow under very low growth irradiances (Cota, 1985; Kirst & Wiencke, 1995; Lacour *et al.*, 2017). This ability to rapidly restore photosynthetic activity after the extended period of darkness during the polar night, exploit low irradiance levels for carbon fixation, and in addition rapidly utilize increasing irradiances is necessary for coping with the high seasonal variability of light in the Arctic (**Paper I and II**). However, these findings do not only concern the autumn and spring transition phases in polar oceans but may also be an important mechanism for phytoplankton overwintering below the euphotic zone of temperate oceans until nutrients get replenished during autumn and winter storms.

Many studies have investigated the impact of irradiance availability on sea ice algae, and the common perception is that sympagic algae exhibit very low light requirements for growth (Thomas & Dieckmann, 2002; Hancke *et al.*, 2018). Within the sea ice in early spring when irradiance levels were low, and nutrients were plentiful, sympagic algae also displayed clear signs of photoacclimation to low light (**Paper II**). They showed increased light utilization (i.e. high FRRf-derived α and low POC:Chl *a* ratios), ensuring maximized absorption of the limited light available within the sea ice. As daily average irradiances increased towards ~8 µmol photons m^{-2} s^{-1}, sympagic algae efficiently decreased light-harvesting coupled with an increased capacity for photoprotection, which seem to be the preferred method of regulating energy flow to PSII (**Paper II**, Alou-Font *et al.*, 2013, Galindo *et al.*, 2017). These light-driven adjustments to the photosynthetic machinery ensured a high level of plasticity in their light-acclimation capabilities in the low daily average irradiance range between 0 and 8 µmol photons m^{-2} s^{-1}. This resulted in increasingly healthy cells (F_v/F_m, Fig. 6a) that were also able to increase their maximum electron transport rates through PSII (ETR_{max}) towards average irradiance levels of ~8 µmol photons m^{-2} s^{-1} (**Paper II**). Surprisingly, even though the sympagic assemblage seemed

well acclimated to low light, the pelagic assemblage was still more efficiently utilizing the low available light for carbon fixation. The *in situ* incubation experiment (**Paper II**) revealed a similar FRRf-based α in sympagic and pelagic algae, however, the ^{14}C based α were half as high in the sympagic algae assemblage (Fig. 6b, c). This indicates that both assemblages were equally efficient in harvesting available light for electron transport through PSII, but sympagic algae were less efficiently transferring this energy into biomass build-up. Photosynthesis must supply photosynthetic resources (such as ATP and NADPH) for all cellular activities, not just carbon fixation. The fraction of ATP and NADPH that is invested in carbon fixation can thus vary with the dominant metabolic activities occurring at a given time (Behrenfeld *et al.,* 2008), and is most likely the key to understand the observed differences in energy allocation between pelagic and sympagic algae. It would make sense that sympagic algae are adapted to extreme conditions of reduced temperature, high salinities and extremely variable nutrient and carbon levels, and allocate more of the photosynthetic resources for associated cellular processes (e.g. cryoprotection, osmoregulation, nutrient transport, carbon concentrating mechanisms). Thus, less of the energy is channeled directly into the Calvin Cycle and subsequent biomass build-up compared to pelagic algae (Behrenfeld *et al.*, 2008). Hence, pelagic algae can remain net productive under extreme low light conditions (**Paper I and II**), possibly explaining the ability of phytoplankton to generate substantial blooms underneath the sea ice (Mundy *et al*., 2014, Assmy *et al*., 2017), where irradiance levels are lower than at the ice-water interface. These recently observed under-ice phytoplankton blooms are therefore possibly not a new phenomenon in ice-covered seas of the Arctic. In fact, Lowry *et al.,* (2014) argue that under-ice blooms in the Chukchi Sea have been common more than a decade prior to their discovery in 2011 (Arrigo *et al.,* 2014b). However, light conditions suitable for under-ice blooms have increased in the past 30 years, so the frequency and prevalence of under-ice blooms could be increasing, and consequently more likely to be discovered (Horvat *et al*., 2017).

4.2 Higher sensitivity towards high light stress in Arctic sympagic compared to pelagic algae

Both pelagic and sympagic algae were effectively acclimated to very low available light, able to use this light for carbon fixation, and quickly exploited increasing irradiances in the low irradiance range as outlined above (**Paper I and II**). However, at higher irradiance levels, we observed substantial differences in the acclimation capacity of the two microalgal assemblages. Pelagic algae exhibited high resilience to instantaneous light stress and high photoacclimative capacity towards increasing irradiances. Sympagic algae, one the other hand, showed higher sensitivity towards the same irradiance ranges (**Paper II and III),** which is in line with previous findings of a detrimental effect of high irradiances on natural sea ice algae communities in Svalbard (Leu *et al*., 2010).

In Van Mijenfjorden during spring and summer in 2017, we followed photophysiological and biochemical characteristics of natural pelagic and sympagic algae communities in order to evaluate strategies used by the two functionally distinct types of microalgal communities to acclimate to variations in irradiance and nutrient levels (**Paper II**). The field observations revealed that natural pelagic communities were able to use additional excitation energy for photochemistry as average daily irradiance levels increased towards ~80 µmol photons m^{-2} s^{-1}, evident by increasing ETR_{max}. At the same time, sympagic algae assemblages showed signs of substantial photoprotective efforts as average daily irradiance increased > 8 µmol photons m^{-2} s^{-1}; light absorption continued to be efficiently lessened and photoprotective mechanisms started to increase more intensively. However, photochemical damage and oxidative stress appeared to overweigh cellular defenses, causing F_v/F_m to decrease, which reached extremely low values under the highest average light (i.e. ~0.1 at 75 µmol photons m^{-2} s^{-1}, Fig. 6a, **Paper II**). The substantial photoinactivation of PSIIs was not sufficient to sustain high rates of electron transport, and so, in contrast with the pelagic community, ETR_{max} decreased with increasingly higher average irradiances > 8 µmol photons m^{-2} s^{-1} (**Paper II**). In **Paper I and III** we observed a strong short-term decrease in τ_{ES} in response to illumination to higher irradiances in pelagic algae, indicating that the increased supply of electrons to the plastoquinone pool was met by a quickly increasing capacity to shuttle the energy away from PSII. Sympagic algae, however, seem to have impaired electron drainage (higher τ_{ES}) towards higher irradiances compared to pelagic algae (**Paper II and III)**, which were also well reflected in the time-course of gene expression (**Paper II**). This efficient energy drainage into carbon fixation in pelagic algae was further corroborated by the fast induction of NPP (**Paper I)** and higher ^{14}C-derived α compared

to sympagic algae during the *in situ* incubation experiment (**Paper II**). Since such electron drainage into carbon fixation helps to prevent high light stress, it can explain the observed higher plasticity (and consistently lower NPQ) observed in pelagic compared to sympagic algae (**Paper II and III**). In line with previous findings, this confirms that light transmittance exerts strong control on sea ice algae, even under low irradiance levels (Alou-font *et al*., 2013; Galindo *et al*., 2017). Even though these studies show that sea ice algae were able to photoacclimate to higher irradiances compared to the observations in **Paper II**, it is important to note that we derived the irradiance levels as the average of 24 h before the sample was taken, which is substantially lower than the experienced peak values. Arctic pelagic algae assemblages, on the other hand, showed high resistance to enhanced irradiance levels, which have been documented many times before (Leu *et al*., 2006; Moore *et al*., 2006; Hoppe *et al*., 2018b).

During the field campaign in Van Mijenfjorden, bottom ice Chl *a* concentrations peaked, surprisingly, at the same time as the peak in pelagic Chl *a* concentrations (**Paper II**). This offered a unique possibility to conduct field experiments and directly compare light-dependent electron transport and carbon fixation towards increasing irradiances in natural pelagic and sympagic communities. The *in situ* incubation experiment conducted underneath the sea ice in Van Mijenfjorden (**Paper II**) also revealed large differences in photoacclimative capacity between pelagic and sympagic algal assemblages. The light saturation parameter for photosynthesis (E_k), is an indicator of the incubation irradiance at which photosynthesis saturates (Sakshaug *et al*., 1997). The FRRf-derived E_k in pelagic assemblages was over twice as high compared to sympagic algal assemblages, and higher than peak irradiances during the incubation period, making them more likely to efficiently acclimate to higher irradiances (Fig. 6b). Furthermore, the constantly increasing carbon uptake rates in pelagic algal assemblages revealed that they were light limited with all irradiances up to ~90 µmol photons m^{-2} s^{-1}, while sympagic algae were not able to take advantage of increased irradiances for carbon fixation beyond ~40 µmol photons m^{-2} s^{-1} (Fig. 6c, **Paper II**). This, together with the field observations, strongly suggests that the sampled pelagic algae were generally light limited during the study period in spring 2017 in Van Mijenfjorden. In comparison, the ability of natural sympagic algal assemblages to take advantage of increases in irradiance was restricted to lower irradiance ranges (**Paper II**), implying community-specific thresholds for high light acclimation. This is in line with findings on higher sensitivity and slower acclimation responses towards high light in a dominant Arctic sympagic diatom compared to pelagic diatom (**Paper III**). *Thalassiosira hyalina* and *Nitzschia frigida* are important members of Arctic pelagic and sympagic diatom

communities, respectively (**Paper II**, Von Quillfeldt *et al*., 2003; Hegseth & Sundfjord, 2008, Leu *et al.,* 2015). We investigated their short-term response, intermediate recovery phase and a re-acclimated state towards a high light scenario of 380 µmol photons m^{-2} s^{-1}, resembling sudden ice break-up or melt pond formation (**Paper III**). The short-term high light induced responses of the pelagic diatom *T. hyalina* were clearly different from the sympagic diatom *N. frigida*, as photosynthetic parameters such as F_v/F_m and α decreased ~8 times faster in the latter (Fig. 7). This dramatic decrease in photosynthetic efficiency of *N. frigida* was probably related to oxidative damage and loss of functional reaction centers, which seemed to overweigh photoprotective efforts and prevent a successful recovery. Even with prolonged exposure to high light (i.e. 120 h), *N. frigida* were unable to acclimate and take advantage of the higher light. *T. hyalina*, however, handled photophysiological stress well and acclimated rapidly (within 72 h) to higher irradiances, leading to increased growth rates and organic carbon quotas under high light conditions (Fig. 7, **Paper III**). These converging recovery responses between the species could be attributed to the fact that *T. hyalina* showed a rapid (i.e. after 2 h) and pronounced downregulation of fucoxanthin-chlorophyll binding proteins (FCP genes), indicating lowered synthesis of light harvesting pigments. In *N. frigida,* however, many FCPs were also upregulated, probably hampering the cells' attempt to reduce photon harvest on short-time scales. In addition, the antioxidative response seemed less effective in the latter (**Paper III**). Hence, the acclimation capacity was remarkably different between the two species, as the pelagic diatom had higher thresholds and faster photoacclimation towards high light compared to the sympagic diatom, which was also validated on the community level (i.e. natural pelagic vs. sympagic communities, **Paper II**). A clear negative impact of high irradiances on natural sea ice algal communities have been documented earlier (Juhl & Krembs, 2010; Leu *et al*., 2010). However, Juhl & Krembs (2010) estimated that the minimum acclimation time required by sea ice algae was relative long (between 3 – 6 days), which was later confirmed by Alou-Font *et al*., (2013). Hence, whether or not successful acclimation could be established on longer time scales or more gradual increases in irradiances remains to be tested.

Underlying reasons for the divergent sensitivities towards high light

Results from **Paper II and III** clearly show that pelagic algae exhibited higher plasticity towards increasing irradiances and were more efficient in draining energy into carbon fixation compared to sympagic algae, both in low and high light. This could be explained by adaption to strongly contrasting irradiance regimes normally encountered by the two algal assemblages. Vertical mixing of phytoplankton cells within deeply mixed surface layers goes along with strong fluctuations in irradiance levels, potentially from darkness to full sunlight (MacIntyre *et al.,* 2000; Fig. 5). Hence, it makes sense that pelagic phytoplankton have evolved pronounced mechanisms into being flexible with different irradiances they encounter (e.g. Behrenfeld *et al.,* 1998). This is in line with the fact that Arctic pelagic phytoplankton assemblages have also been shown to be rather resistant to changes in temperature, irradiance and pCO_2, a finding that has been explained by the high environmental variability they have to cope with (Hoppe *et al.,* 2018a). Compared to the strong fluctuations in light regimes pelagic algae encounter, sympagic algae usually experience irradiances on lower amplitudes (Hill *et al.*, 2018; Fig. 5). Irradiance reaching the bottom of sea ice is principally regulated by ice thickness and overlaying snow cover, where the latter is usually most important due to its high light attenuation properties (Mundy *et al*., 2005, Marks & King, 2014). As a result, reported transmittance through ice and snow layers in the Arctic is often very low. Since microalgae cells will mostly acclimate to their average experienced growth environment (Behrenfeld *et al*., 2008), it explains the observed differences in sensitivity towards high light scenarios between pelagic and sympagic algae (**Paper II and III**). Furthermore, pelagic algae could also experience fluctuations in light intensity with much higher frequency compared to sympagic algae. Sympagic algae live in a spatially restricted environment that is normally not undergoing rapid changes, so they usually experience more gradually changing irradiances (e.g. gradual changes in the suns elevation and snow cover overlaid by diurnal fluctuation) compared to pelagic algae where vertical mixing can induce large variations in light regimes within minutes. Furthermore, fluctuations due to weather conditions are most extreme in the high light range, so the effect of rapid shifts in cloud cover is more important in the uppermost part of the water column than at the ice-water interface (Fig. 5). Sea ice algae are known to persist at extreme environmental properties such as high salinities, sub-zero temperatures, low nutrient levels as well as distorted carbonate chemistry (Weeks & Ackley 1986, Aletsee & Jahnke 1992, McMinn, 2017), and in addition show high photophysiological and phenotypic plasticity in response to changes in temperature and salinity (Petrou *et al*., 2011). Hence, sympagic algae seem to allocate more of the photosynthetic resources in tolerating extreme conditions within sea ice (also seen in the lower energy

conversion in sympagic vs. pelagic algae discussed in chapter 3.1), rather than dealing with large and rapid fluctuations in light regimes.

In Van Mijenfjorden (**Paper II**), ecophysiological responses towards variations in irradiance levels were generally subtle or even absent in natural pelagic algal assemblages, while the sympagic assemblages showed stronger trends towards the same average daily irradiance ranges. These contrasting responses could possibly also be explained by the temporal development in the taxonomic composition (Suggett *et al*., 2009). Arctic phytoplankton communities can be very dynamic and diverse, and taxonomic changes are mostly driven by temporal variability in light and nutrient levels (Marquardt *et al.,* 2016). During the polar night, we found diverse and active marine phytoplankton communities consisting of both autotrophic and heterotrophic species, the latter being more prevalent in January 2015 (**Paper I**). The winter in polar marine environments is particularly challenging for phototrophic primary producers, and hence, the importance of heterotrophic species during the polar night was as expected (**Paper I,** Brown *et al*., 2015). In **Paper II**, the pelagic community was often very heterogenous (i.e. mixed dominance between groups) as well as dynamically changing between dates, stations and depths. In spring, communities underneath the sea ice in van Mijenfjorden were mostly dominated by diatoms and *Phaeocystis pouchetii*, which are known to prevail under low growth irradiances (Assmy *et al.*, 2017; Lacour *et al.*, 2017). Later in June and August, when NO_3 and SiO_4 levels were depleted, diatoms were outcompeted by *Phaeocystis pouchetii* which have lower or no requirements for these nutrients compared to diatoms (Egge & Aksnes, 1992; Jiang *et al.*, 2014), and other flagellate species that have different energy acquisition strategies (autotrophy vs. heterotrophy, **Paper II**). This strongly suggests that taxonomic changes within the pelagic community were driven by selection of species that were better adapted to the prevailing light and nutrient environment (Cullen & MacIntyre, 1998). Hence, shifts in the assemblage composition could make the pelagic community rather resistant to changes in environmental parameters (Hoppe *et al*., 2017), possibly explaining the absent to subtle trends towards variations in irradiance (and nutrient levels) in Van Mijenfjorden (**Paper II**). In comparison, the sympagic algal assemblage was much more homogenous, i.e. strongly dominated by pennate diatoms across stations and dates. The resupply of new species was thus restricted in the sympagic realm, potentially causing generally lower diversity and plasticity towards changing environmental conditions (**Paper II**).

4.3 Interacting environmental variables increase sensitivity towards light stress

As outlined in the sections above there are clear differences in photophysiological characteristics between pelagic and sympagic algae, probably due to evolutionary adaption towards very different niches. It is increasingly evident, however, that synergistic and antagonistic interactions among multiple drivers are essential to provide more realistic predictions of future ecosystems changes, especially since changes in one environmental condition is often accompanied by changes in others (Riebesell & Gattuso, 2015). Also, during late bloom phases, microalgal growth is often limited by several factors, e.g. nutrient limitation and photoinhibition (Lavoie *et al.*, 2005; Galindo *et al.*, 2017; Mortenson *et al.*, 2017). Nitrogen limitation may have considerable effects on microalgal physiology, because synthesis of proteins (such as D1 and Rubisco) and pigments requires nutrients (Eberhard *et al.*, 2008). NO_3 starvation can thus impede photoacclimation responses (Geider *et al.*, 1993; Van De Poll *et al.*, 2005), thereby increasing susceptibility to photoinhibition (Kiefer, 1973; Litchman *et al.*, 2002). Moreover, nutrient limitation affects photochemical energy conversion as energy derived from light reactions may be used for nutrient uptake rather than carbon fixation (Kulk *et al*., 2018). In Van Mijenfjorden (**Paper II),** the highest photosynthetic efficiency of sympagic algae was observed when light was low and NO_3 concentrations were high. The abundant NO_3 supply probably supported biosynthesis of photosynthetic pigments (Eberhard *et al*., 2008), and thus ensured maximized absorption of the limited light available beneath the sea ice. Under the highest light, concurrent nutrient limitation impeded photoacclimation and contributed to the strongly reduced photosynthetic efficiency observed in sympagic assemblages in this study, indicating that the combined stressors impose negative synergistic effects in sympagic microalgal communities (**Paper II**). In pelagic assemblages, however, no notable trends in physiological or biochemical parameters were observed with decreasing NO_3 levels (**Paper II**). The pelagic algal assemblages encounter more small-scale resupply (e.g. from vertical mixing) that occurs in the sympagic realm, meaning that even though the measured nutrients were similarly low in ice and open water, nutrient limitation was probably still occurring over a longer period in the sympagic algal assemblages. This could explain the differential responses in the two algal assemblages. Furthermore, POC has been shown to be largely decoupled from Chl *a* concentrations when significant contribution of organic carbon comes from heterotrophic/mixotrophic production (Niemi & Michel, 2015). Given the heterogenous pelagic community composition, which was also dynamically changing, it could explain the highly variable POC:Chl *a* and C:N, and subsequent lacking trends with NO_3 levels in **Paper II**.

Many studies have shown that responses to changing light intensities can be modulated by high pCO_2 (Rost *et al.*, 2006; Rost *et al.*, 2008; Li & Campbell, 2013; Hoppe *et al.*, 2015). The results, however, have been partly divergent indicating large inter- and intraspecific differences in CO_2 sensitivity. Hence, it has been suggested that OA may significantly alter phytoplankton species composition (Leu *et al.*, 2013; Gao & Campbell, 2014). In **Paper III**, we observed some similarities between the responses of the pelagic diatom *T. hyalina* and the sympagic diatom *N. frigida* to CO_2 enriched conditions, such as growth inhibition under high light and high pCO_2, hinting towards a higher sensitivity for the combination of the two stressors. The concomitant increase of H^+ levels seemed to impair overall cellular homeostasis, making it more difficult for cells to adjust redox harmonics. Thus, despite the species´ different capacities to cope with high light stress, OA seems to impose additional stress that requires more intense regulatory efforts. In addition, there were also large differences in sensitivity towards high pCO_2 under low light conditions between the two diatoms, implying species-specific differences in the sensitivity towards OA (**Paper III**). Our findings from **Paper II and III** clearly highlight the importance of considering interactive effects of environmental variables, but also show the value of comparing differently adapted species and functionally distinct algal assemblages.

4.4 Future implications

The results from this thesis imply that both taxonomic composition and the physiological acclimation of these taxa to variable environmental conditions must be considered when assessing photosynthetic performance in algal assemblages. Despite such underlying dynamics, however, we see clear differences in the acclimation potential of natural pelagic and sympagic algae communities (**Paper II**), that align well with specific physiology of key species of these habitats (**Paper III**) as well as the environmental conditions they have adapted to (**Paper I, II and III**). Pelagic algae are well adapted to variable light conditions experienced in the wind-mixed pelagic environment, ensuring high rates of light-dependent photosynthesis and carbon fixation under a wide range of irradiance levels (**Paper I, II and III**). Sympagic algae, however, which were more sensitive towards higher irradiances, had to allocate more energy into photoprotective mechanisms and alternative energy sinks (e.g. photorespiration, Mehler reaction, cyclic electron transport through PSI). In addition, sympagic algae seem to use more of the photosynthetic resources for tolerating extreme environmental conditions within sea ice, which in return resulted in lower rates of linear electron transport and carbon assimilation compared to pelagic algae (**Paper II and III**). Consequently, there might be substantial

differences in the responses of pelagic vs. sympagic microalgae towards climate change in Arctic marine systems. The accelerating decrease of Arctic sea ice extent and thickness will not only open large new areas for phytoplankton primary production but also increase under-ice light intensities. Pelagic microalgal assemblages, with its high resilience towards environmental changes (**Paper I, II and III**), will likely continue to be major primary producers in the pelagic realm. Additional loss of Arctic sea ice is furthermore expected to increase phytoplankton productivity due to longer growing seasons (Arrigo *et al.,* 2008). At the same time, the effect of high light intensities might be substantial in sea ice assemblages where life is rather adapted to low light conditions, and in addition show higher sensitivity towards a combination of multiple stressors (**Paper II and III**). The importance of ephemeral sea ice (i.e. melting and re-forming each year) is likely to increase in the future (Onarheim *et al*., 2018), and consequently, organisms inhabiting the sea ice will have to deal with much more dynamic environmental settings. This could result in a decrease in fitness of sea-ice algae, potentially decreasing their relative contribution to biomass and annual primary production in a future Arctic. Although carbon fixation rates tend to be lower in sympagic compared to pelagic algae (**Paper II and III**), their ecological significance is still high. Sea ice algae are an essential high-quality food source for herbivores early in the season and in addition fuel maturation and reproduction of the key Arctic species *Calanus glacialis* (Søreide *et al*., 2010). Furthermore, rapidly sedimenting sea ice algae represent an important food source for benthic grazers and filter feeders (Boetius *et al*., 2013, Renaud *et al*., 2007), and play a major role in in the global carbon cycle by removing carbon from upper ocean and atmosphere. The detrimental effect of high irradiances on sea ice algae could thus have important implications for trophic interactions, carbon fluxes and budgets.

Chapter 5

Conclusion

Predicting how phytoplankton communities will reorganize in the future in response to multifaceted simultaneous changes to their environment, is currently a major scientific challenge, vital for predicting ecosystem function and conservation. The Arctic ocean is changing fast in many respects, amongst which temperature, sea ice cover and pCO_2 stand out as being those changing most rapidly. Consequently, irradiance levels under ice and in surface waters are expected to increase and nutrient regimes are expected to change due to increased stratification and reduced mixed layers. In addition, atmospheric pCO_2 is rising, leading to elevated concentrations of CO_2 and lowered pH in the seawater. Due to all the ongoing and predicted changes it is obvious that productivity in the Arctic is going to change – but still, there is very little reliable information available on that, and modeling attempts are limited. Our results show that synergistic and antagonistic interactions among multiple drivers need to be considered when predicting future productivity and ecosystem functioning. Furthermore, our results have important implications for the current understanding of how Arctic algal blooms might change in the context of climate change. This study suggests that the balance between sea ice-based vs. pelagic primary production could change with respect to timing and quantity in a future Arctic, with important implications for higher trophic levels and the biological carbon pump. Especially in model-based scenarios of future Arctic algae blooms, parametrization of sea ice algal vs. phytoplankton-derived primary production needs to include such functional differences of algal communities.

Considering the substantial differences in sensitivity between pelagic and sympagic algae seen in this study, I strongly argue for further research comparing these two functionally distinct groups of microalgae towards changes in the abiotic environment. Furthermore, more information about the impact of environmental parameters on the food quality of pelagic and sympagic algae, in addition to trophic interactions in the high Arctic is needed to make thorough predictions of implications on downstream food webs. Clearly, more long-term studies covering several seasons are needed to detect changes and baseline shifts and gain a more mechanistic understanding of response patterns in pelagic and sympagic algal assemblages. Knowledge of such temporal changes in microalgal biomass and primary production is key for a better understanding of polar ecosystem structure and function.

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Section II

Research papers

Kvernvik AC, Hoppe CJM, Lawrenz E, Prášil O, Greenacre M, Wiktor JM, Leu E. 2018. Fast reactivation of photosynthesis in arctic phytoplankton during the polar night. *Journal of Phycology* **54**:461-470

Paper I

Kvernvik AC, Hoppe CJM, Greenacre M, Verbiest S, Gabrielsen TM, Reigstad M, Leu E. Arctic sea ice algae differ markedly from phytoplankton in their ecophysiological characteristics. *Manuscript in preparation for submission.*

Paper II

Kvernvik AC, Rokitta SD, Leu E, Harms L, Gabrielsen TM, Rost B, Hoppe CJM. In review. Higher sensitivity towards light stress and ocean acidification in an Arctic sympagic compared to a pelagic diatom. *Submitted to New Phytologist*.

Paper III