

Chapter 4

Marine micro- and macroalgae in the Arctic Polar Night

Geir Johnsen, Eva Leu and Rolf Gradinger

Abstract The chapter elucidates aspects of the ecology of micro- and macroalgae with a focus on the dark season. It comprises of six parts and starts with an introduction (4.1) about Arctic marine micro- and macroalgae. Section 4.2 reviews the key abiotic environmental variables related to micro- and macroalgae growth and survival. The description of the different groups of microalgae are shown in section 4.3, comprising phytoplankton, microphytobenthos and sea-ice algae. Section 4.4 describes the three classes of macroalgae (phaeo-, rhodo- and chlorophytes) with information about biological variables, seasonal processes and habitats. Section 4.5 describes the ecophysiology of microalgae and macroalgae in the Polar Night. The last section 4.6 gives conclusive remarks of what we know and don't know with suggestions for future research. Microalgae have unique adaptations including life cycles and ecophysiology that allows them to rapidly grow once light comes back in spring, while some macroalgae can utilize the Polar Night for growth. For microalgae, resting stages and mixotrophy appear to be adaptive traits to survive the winter season. In contrast, some macroalgal species may act as "season anticipators" and utilize the winter darkness or initial spring period as major growth seasons. We still lack basic knowledge about the overall biodiversity, ecology and physiology of microalgae and both annual and perennial species of macroalgae during the winter months.

G Johnsen

Centre of Autonomous Marine Operations & Systems (AMOS),
Trondhjem biological station, Dept. Biology, Norwegian University of Science
& Technology (NTNU), N-7491 Trondheim, Norway.
Email: geir.johnsen@ntnu.no

E Leu

Akvaplan-niva AS, CIENS, Gaustadalleen 21, N-0349 Oslo, Norway
Email: eva.leu@akvaplan.niva.no

R Gradinger

UiT Norges Arktiske Universitet, P.box 6050 Langnes,
N-9037 Tromsø, Norway
Email: rolf.gradinger@uit.no

4.1 Introduction

Primary production is the ability of plants and algae to convert inorganic C (CO₂) to organic C in the process of photosynthesis, using light as the energy source. Thereby, primary producers form the basis of the entire food web, as it is ultimately the biomass that they produce that serves as food for higher trophic levels. As a consequence, seasonal fluctuations in light availability do not only impose strong limitations on primary producers, but have propagating effects along the entire Arctic food chain (Falkowski and Raven 1997). In the Arctic, micro- and macroalgae are the main primary producers, providing organic matter (food) to all trophic levels. Here, higher plants, moss and lichens on land contribute very little to the overall production of organic material. Since most of the primary production occurs in the ocean, there is a large and crucial transport of organic matter from ocean to land through e.g. Arctic seabird rookeries or walrus colonies. Chapter 3 focuses on the Arctic light climate and “darkness” during Polar Night, which is highly relevant for the eco-physiology and corresponding nutrient mode of algae (Fig 3.1). In this chapter, we describe how micro- and macroalgae cope with this extended period of “darkness” they experience during the Polar Night. Microalgae are unicellular organisms occurring in various habitats in Arctic seas and belong to a range of taxonomic groups. They can be divided according to their habitat: Phytoplankton in open waters (pelagic), microphytobenthos (seafloor), sea ice algae (sympagic) as well as algae growing on other algae (epiphytic) or animals (epizoic).

Microalgae encompass different taxonomic groups that are each characterized by a distinct pigment composition and may be found as single cells or as colonies in the water column or attached to substrates as sea-ice and soft bottom seafloor (Table 4.1, following the class- and pigment chemotaxonomy of Jeffrey et al. 2011). The main ecologically important eucaryotic classes belong to the kingdom Chromista (Chromophyta), i.e. Chlorophyll (Chl) c-containing algae. For microalgae the Chromista comprises Bacillariophyceae (diatoms), Dinophyceae (dinoflagellates), Coccolithophyceae (prymnesiophytes in Haptophyta), Chrysophyceae (chrysophytes), and Cryptophyceae (cryptophytes). Chlorophyll b-containing microalgal classes belonging to Plantae include chlorophytes, prasinophytes and the euglenophytes. The third major pigment group consists of the procaryotic phycobiliprotein-containing Cyanobacteria (bacteria) and the previously mentioned cryptophytes. All of these classes do have marker pigments (group-specific pigment indicators), either belonging to the chlorophylls, carotenoids or phycobiliproteins (Fig. 4.1; Table 4.1; see also pigment signatures in Chapter 3).

Benthic macroalgae (“seaweeds”; Lüning 1990) are macroscopic, multicellular organisms, mainly living on hard substrate on the seafloor, and are found within coastal intertidal and sub-tidal zones. They also have class-specific differences in pigment composition that are reflected in their names (brown, green and red macroalgae), and which determine which wavelengths of visible light (400-700 nm) they can absorb and further utilize. Macroalgae comprise three pigment groups: the class Phaeophyceae (Chl c-containing brown algae, also belonging to Chromista), the phylum Rhodophyta (Rhodophyceae, comprising phycobiliprotein-containing red algae) and the phylum Chlorophyta (Chl b-containing green algae, Fig. 4.2; Table 4.1, see also reviews by Wiencke et al. 2007; Wiencke 2011; Hurd et al. 2014).

Algal pigment composition (Table 4.1) may contain information about phylogenetic relations (chemotaxonomy, Jeffrey et al. 2011; Rowan 1989) and physiological/functional characteristics, such as light harvesting pigments (LHP), related to species-specific habitats and depth, and photoprotective carotenoids (PPC). In addition, the pigment composition determines the *in vivo* light absorption characteristics of different algal classes from which we can derive

their utilization of light at specific wavelengths, bio-optical taxonomy and the health status of chloroplasts of micro- and macroalgae (see also Chapter 3 and 10).

Table 4.1. Major pigment groups of micro- and macroalgae found in the Arctic. Major light harvesting pigments (LHP) and photoprotective carotenoids (PPC) in micro- and macroalgae with the corresponding *in vivo* absorption peaks discriminating between them are shown. Spectral *in vivo* light absorption and their relation to major pigments are indicated: absorption in blue part of the solar spectrum (481 nm), green (535 nm), orange (586 nm) and red (649 nm). Note that Chl a is found in all groups and therefore not used as a discriminator. Chromista denotes Chl c-containing algal classes and Chlorophyta denotes Chl b-containing classes. Microalgae adapted from Johnsen et al 1994, 2011; Jeffrey and Vesk 1997; Edvardsen et al. 2007; Jeffrey et al. 2011. Macroalgae adapted from Rowan 1989; Grzymiski et al. 1995; Esteban et al 2009.

		481 nm	535 nm	586 nm	649 nm
		LHP + PPC	LHP	Chl c and b	Chl b
MICROALGAE	Chl c-containing microalgae				
	Diatoms	DD,Fuco	Fuco	Chlc ₁₊₂	-
	Dinoflagellates	DD,Peri/Fuc+19F	Peri/(Fuco+19F)	Chlc ₂₊₃	-
	Haptophytes	DD,Fuco,19F	Fuco+19F	Chlc ₂₊₃	-
	Chrysophytes	DD+Fuco	Fuco	Chlc ₂	-
	Raphidophytes	Fuco,Viola,Zea	Fuco	Chlc ₁₊₂	-
	Dictyophytes	DD,Fuco,19F	Fuco,19F	Chlc ₁₊₃	-
	Chl b-containing microalgae				
	Prasinophytes	Pras/Lut, Viola,Zea,Chlb	Pras	Chlb,MgDVP	Chlb
	Euglenophytes	DD,Neo,Chlb	-	Chlb	Chlb
	Chlorophytes	Viola,Zea,Lut,Chlb	-	Chlb	Chlb
	Prochlorophytes	DV-Chlb,Zea,β-car	-	DV-Chlb	Chlb,DV-Chlb
	Phycobiliprotein phytoplankton				
Cryptophytes	Allo	PE	Chlc ₂	-	
Cyanobacteria	PBP,Zea,β-car	PBP	-	-	
MACROALGAE	Brown algae	Fuc,Viola,Zea,Neo	Fuc	Chlc ₁₊₂	-
	Red algae	PBP,Lut,Zea	PBP	-	-
	Green algae	Chlb,Lut,Zea,Anth,Neo	-	Chlb	Chlb

Table abbreviations: PPC: diadino- and diatoxanthin (DD), zeaxanthin (Zea). LHP: Chlorophyll b (Chlb), Chlorophyll c (Chl c1, Chlc2, Chlc3), Magnesium 2,4-divinyl phaeoporhyrin as monomethylester (MgDVP), divinyl Chl b (DV-Chlb), Fucoxanthin (Fuco), 19'-acyl-oxy-fucoxantins (19F), peridinin (Peri), violaxanthin (Viola), antheraxanthin (Anth), prasinoxanthin (Pras), lutein (Lut), neoxanthin (Neo), alloxanthin (Allo), β,β-carotene (β-car). Phycobiliproteins (PBP), note that PBP comprises several pigments and often dominated by phycoerythrin absorbing in green part of spectrum.

As for all primary producers, algal distribution and seasonality is controlled primarily by the availability of light and nutrients (Fig. 4.1). Light is absorbed, reflected and scattered in water and sea ice depending on their inherent optical properties (Chapter 3), and the lower limit of habitable environments for algae is considered the deepest part of the so-called photic zone. Primary producers also consume inorganic nutrients, that are re-suspended from deeper waters and/or sediments during mixing events that might occur episodically (e.g. due to strong wind events, or upwelling), or more regularly on a seasonal basis, usually in wintertime in absence of water mass stratification (Fig. 4.1). For certain times of the year, nutrients are contributed through regeneration of organic material in a microbial food web.

4.2. The key abiotic environmental variables related to micro- and macroalgae

Similarly to microalgae, occurrence and seasonal patterns of macroalgae are a function of the environmental conditions, and are as such highly dynamic and complex. The environmental variables are further discussed with a focus on Polar Night eco-physiology (4.5) using examples of microalgae (4.5.1) and two kelp species as case studies (4.5.2). The 11 main key environmental (abiotic) variables that affect micro- and macroalgae are as follows:

1. **Light climate** (intensity, wavelength and photoperiod, see details in Chapter 3, Fig 4.1).
2. **Inherent and apparent optical properties** (AOP, IOP, Chapter 3).
3. **Sedimentation** (freshwater run-off, re-suspension, plankton, marine snow (Chapter 2).
4. **Temperature** (Chapter 2).
5. **River run-off** (reducing salinity and enhancing turbidity and osmotic stress, Box 4.1).
6. **Sea-ice** (changing habitats, light attenuation, ice scouring, Fig. 4.1, Box 4.1).
7. **Nutrients** (micro and macro nutrients, Fig 4.1).
8. **CO₂ availability** (related to photosynthesis, respiration ice and winter survival, Fig. 4.2).
9. **Wave action and current speed/direction** (also related to ice cover, Fig. 4.2).
10. **Substrate exposure and type** (Fig 4.2-3, Box 4.2).
11. **Ocean current system** (e.g. Atlantification, Chapter 2).

The intensity and duration of irradiance (E) in the visible part of the solar electromagnetic spectrum (E_{PAR} , 400-700 nm, often termed photosynthetic active radiance, PAR) and $E(\lambda)$ (spectral irradiance) will define the photoperiod (day length, note that this is highly species, time and space dependent for a given algal cell or chloroplast). The **light regime** (light climate), comprising E_{PAR} , $E(\lambda)$ and photoperiod are detailed in Chapter 3. Note that the photoreceptors in algae, sensitive to the red, green and blue (RGB) part of the solar spectrum, are important in regulating functional genetics such as down- or up regulating the photosynthetic machinery and growth in algae (Nymark et al. 2009, 2011; Valle et al. 2014). This information is then related to species specific absorption of light harvesting pigments in photosystems PS II and I and further photosynthetic light utilization (spectral photosynthesis) of ambient light in microalgae (Johnsen and Sakshaug 2007) and macroalgae (Grzyski et al. 1997), see review in Johnsen et al. 2011). The photoperiod is a major cue for growth for both micro- and macroalgae and will be discussed in section 4.4 and 4.5 (Fig 4.1 A-B). **Competition for light** by photosynthesizing algae limits and defines their vertical distribution in the water column, such as brown algae growing in the well-lit zone from surface to 30 m depth, while red calcareous algae are found down to 50-60 m depth in Svalbard. The vertical extension of the photic zone has been defined traditionally by the 1% light depth relative to surface irradiance and varies from 30-60 m depth in clearer ocean water (Sakshaug 2004; Sakshaug et al. 2009; Assmy et al. 2017) to only few dm to meters in turbid coastal waters receiving land or glacial runoff. A more modern approach is the use of isolumes (Chapter 3) to define the habitat that is potentially usable for algal growth:

this concept focuses rather on a specific light level (often integrated over a certain time) that is necessary for supporting positive net primary production. Its exact level depends on physiological adaptations of the algae. Absolute irradiance (light intensities, E_{PAR}) during summer at the surface of the ocean, leads or snow covered sea ice can exceed $1500 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (Assmy et al. 2017; Kauko et al. 2017, 2018; Zolich et al. 2018) while the lowest limits for algal growth were determined for sea ice algae to be E_{PAR} of 0.2 to $0.4 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (Hancke et al. 2018; Mock and Gradinger 1999).

Typically, water transparency is high during the cold Polar Night when riverine and glacial freshwater run-off is at its minimum due to frozen glaciers, typically from October to June in Svalbard. In the well-lit season from June to October, corresponding with **rising temperatures**, the coastal waters are turbid mainly due to **fresh water sediment transport** (part of the IOPs; Chapter 3) from the glacial rivers and causes reduced light intensity, wavelengths available for light harvesting pigments and reduction of daylength altering photosynthetic performance in both phytoplankton, sea-ice algae, microphytobenthos and macroalgae. Also, sedimentation of mineral particles may also cover micro- and macroalgal surfaces and biofilm, especially larger kelp species, that may be buried in sediments causing them to die, while microphytobenthos may move towards the sediment surface. Low salinities induce **osmotic stress** for both micro- and macroalgae during summer months due to fresh water run-off which is, in contrast, close to nil during the Polar Night.

The seasonal changes and dynamics in **ice-scouring** affects species diversity, primary production and biomass of macroalgae and microphytobenthos (Fig 4.2; Box 4.1; Bartsch et al. 2016). During winter and spring (Oct-May) fjord ice and coastal areas along coast and islands may be attached to the shore line as land fast ice, pack ice (annual sea-ice, 1-2 m thick), multi-year old ice (2-5 thick) or ice bergs from glaciers. Less and thinner **sea-ice** will also change ice algae and phytoplankton dynamics in all aspects (primary production, biodiversity and biomass). Note that there is no distinct zonation of macroalgae in Svalbard in contrast to mainland Europe. This is caused by abiotic and biotic variables in combination, see section 4.4.3 (Box 4.1 and 4.5; Fig 4.2-3).

During high photosynthetic activity during summer time the **macronutrients** (nitrate, nitrite, phosphate and silicate) will be depleted by phytoplankton in competition with macroalgae (Fig 4.1). In contrast, during the Polar Night, ample winter concentrations of nutrients will be of importance for growth in the dark by some of the perennial macroalgae, especially the kelp species *Laminaria solidungula*, detailed later in this chapter. During the phytoplankton bloom period in spring (April-June), high primary production of microalgae and in the kelp forest may induce **CO₂-limitation**, due to photosynthetically CO₂-uptake rising the sea water pH > 9, indicating inorganic C limitation for photosynthesis (Olsen et al. 2006). The pH and [CO₂] are highly light regulated through the effect of photosynthesis (CO₂ uptake and O₂ release) and respiration (CO₂ release and O₂ consumption) on the ocean's inorganic carbon system. The dynamical uptake of nutrients and elements from water are highly dependent on the thickness of the sea surface microlayers around phytoplankton cells and macroalgal lamina which is also affected by **current speed/direction, wave movements and tidal cycle** (Kleiven et al. 2019). During the Polar Night, the whole water column provides ample amounts of CO₂ for macroalgal assimilation during growth (Scheschonk et al. 2019). For macroalgae, **habitats that are protected from or exposed to strong current or wave action** will differ in terms of species composition, zonation, phylogeny (morphological appearance, Lund et al. unpublished) and the eco-physiology of the macroalgae present. The **bottom substrate** (soft vs hard bottom), important for kelp forest growth and survival, is highly affected by current speed/direction, wave action, water depth, time of year and river run-off and particle loading. During the Polar Night, all these potential stress factors may be minimized if a given kelp forest is under sea-ice hindering rough wave action and with no effects from fresh water run-off making clear waters

(low turbidity) and with full salinity (no osmotic stress for organisms). The increased inflow of warm and saline waters into the Arctic from the Atlantic Ocean, the so called “**Atlantification**”, does not only transfer heat to the Arctic, but a higher influx of Atlantic waters causes a higher transport of sub-Arctic and boreal species to the high Arctic which has been observed at summer time (chapter 2) and during the Polar Night (Berge et al. 2015a,b,c).

Knowledge of the abiotic environmental variables and the corresponding biotic variables (discussed in next section) are highly important to understand Polar Night survival and growth strategy for algae.

Microalgae growth and biomass undergo extreme seasonal variations, with bloom formations during the productive spring/summer period, but extremely low abundances during the Polar Night in the water column (Table 4.2, Fig. 4.1; Leu et al. 2011,2015; Vader et al. 2015; Kvernvik et al. 2018) and sea ice (Gradinger et al. 2009). In contrast, biomass and biodiversity of perennial macroalgal species remain high during the winter months with some species continuing to grow, as detailed later in this chapter (Fig.4.2-3, Wiencke et al. 2007; Aamot et al. 2014; Bartsch et al. 2016; Scheschonk et al. 2019; own observations 2010-2018). These different strategies are a result of diverse evolutionary adaptations to the challenge of enduring a prolonged period without light (Polar Night) and reflect some major differences between micro- vs. macroalgae (Fig 4.1) as discussed later in this chapter. The biotic variables important for macroalgae and their impact on algal eco-physiology are discussed in section 4.4.1.

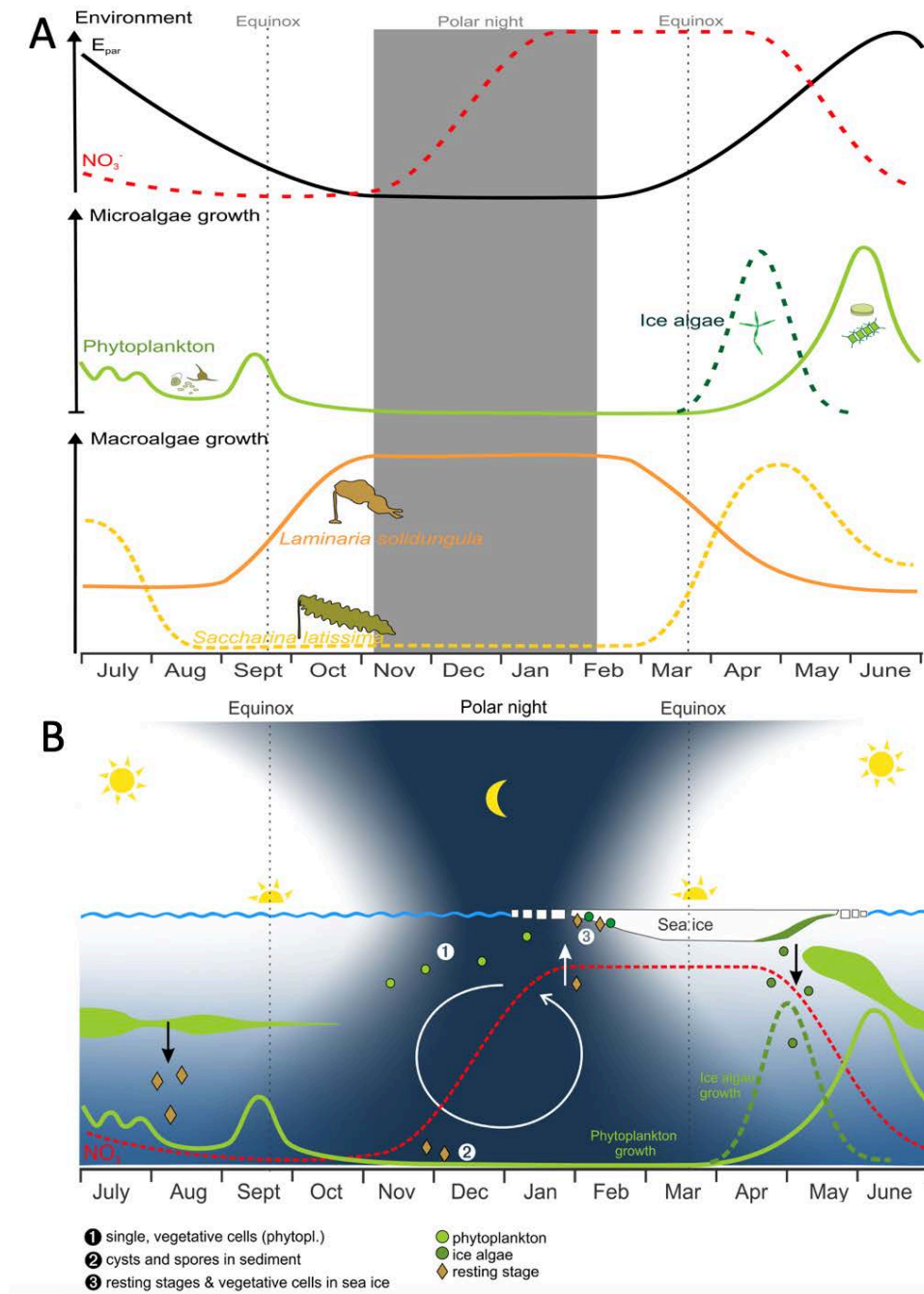


Fig 4.1 A: Seasonal variability of the limiting nutrient concentration (illustrated by nitrate, NO_3^- in upper panel) and irradiance (E_{PAR}) for algal growth. Idealized seasonal growth curves for typical representatives of sea ice algae and phytoplankton (middle panel), and for two kelp species (*Saccharina latissima* and *Laminaria solidungula*) with different growth strategies (lowest panel). B: Distribution and state of microalgae during the Polar Night, and the seasonal context throughout an entire year. During the Polar Night, microalgae can be found as vegetative cells in very low densities in the water column (1), as well as resting stages in surface sediments (2), or in either state inside sea ice (3). All three sub-groups serve as seeding populations for the spring blooms that are initiated once there is sufficient light available. Non-stratified water masses are overturning during wintertime, replenishing the nitrate reservoirs (red dotted curve) in surface waters and thereby preparing the ground for next year's algal spring blooms. Illustration: Malin Daese.

4.3 Microalgae

Marine microalgae in high latitudinal ecosystems experience large seasonal variations in biomass, diversity and production as a consequence of the strong variations in light availability throughout a polar year (Fig 4.1; Chapter 3). Most of the annual primary production of Arctic microalgae takes place during a relatively short period in spring-early summer, when enough sunlight and nutrients are available to allow photosynthetic carbon fixation. Since this biomass represents the basis for the entire food web, the timing, quantity, species composition and food quality of those algal spring blooms is of paramount importance for overall ecosystem productivity. The prolonged period of darkness poses severe challenges for the survival of all phototrophic primary producers including microalgae (Kvernvik et al. 2018). Cell numbers of algae in water and sea ice are much lower during this period, but diversity is often similarly high as during the productive season (Horner and Schrader 1982; Leu et al. 2011, 2015, Niemi et al. 2011). Despite their low biomass and (almost) absent primary production during the winter months, the surviving microalgae are of key importance for the following spring bloom, since the few viable cells represent the inoculum for the production of the following year. In ice-covered seas, the first algal bloom in spring is usually occurring in the lowermost part of the sea ice, followed later on by the pelagic bloom in the water column that can be found already under sea ice (Fig. 4.1, 4.4; Leu et al. 2015; Kauko et al. 2017, 2018; Olsen et al. 2017; Johnsen et al. 2018) but also in open water. The seed population for an ice algae bloom may be found within the sea ice, and can also originate from both pelagic and benthic habitats, dependent on the water depth and vertical mixing processes. In areas with older multi-year ice, colonization of fresh ice may start from horizontally spreading algal cells from repositories in MYI (see details in Olsen et al. 2017; Kauko et al. 2018). Phytoplankton blooms start from cells that have overwintered in the water column, resting stages from sediment surfaces that get re-suspended in the water column due to turbulent mixing, and can also be seeded partly by cells released from melting sea ice. Such complex life cycles involving fast growing vegetative cells during spring bloom but also long-lasting resting stages have been described for often dominating Arctic diatoms and dinoflagellates (e.g. the dinoflagellate *Polarella glacialis* or diatoms of the genera *Thalassiosira*, *Chaetoceros* and *Fragilariopsis*).

4.3.1 Phytoplankton

Towards the end of the productive light season, growing conditions for algae deteriorate, nutrients are depleted, and light gets limiting. During this phase, many phytoplankton species change their metabolic patterns, start accumulating lipid reserves, and/or form resting stages (spores/cysts) that sink to the bottom of the seafloor, or might be embedded in forming sea ice (Olsen et al. 2017). A low abundance of vegetative cells stays in the water column throughout the dark period of the year as well. During the civil Polar Night, which in the Svalbard Archipelago lasts from the middle of November to the end of February (Chapter 3), low cell numbers of pelagic small photosynthetic pico- and nano-eukaryotes are found, even if solar irradiance is well below the detection limit of standard light measuring instruments. Using special methods to quantify Polar Night low light conditions, Cohen et al. (2015) and Ludvigsen et al. (2018) detected peak surface irradiances (E_{PAR}) $\ll 15 \times 10^{-6} \mu\text{mol photons m}^{-2}$

$^2 \text{ s}^{-1}$ (Chapter 3), which are insufficient to support *in situ* primary production, even very close to the sea surface (Kvernvik et al. 2018).

During winter time, the upper water column in coastal waters is characterized by rather uniform temperature and salinity, since this is also the period of complete turnover by vertical mixing, thereby replenishing the nutrient reservoir in the surface layers. As a consequence of lacking vertical gradients in the water column microalgal biomass tends to be distributed rather evenly, with few detectable peaks on *in situ* Chl *a* fluorescence vertical profiles (unpublished results; Fig 4.1). Small, flagellated cells are dominating, often with a high proportion of mixo- and heterotrophic species (Brown et al. 2015; Blachowiak-Samolyk et al. 2015; Vader et al. 2015). Dinoflagellates are one of the dominating classes during this period of the year, and represented by several species of *Protoperdinium*, *Gymnodinium*, *Gyrodinium*, *Dinophysis*, and *Ceratium arcticum* (Blachowiak-Samolyk et al. 2015; Kvernvik et al. 2018; Marquardt et al. 2016). However, in addition to those, some of the most dominant autotrophic species have been found to be widespread throughout the entire year, such as the prasinophyte *Micromonas pusilla*, and the prymnesiophyte *Phaeocystis pouchetii* that is one of the key players during Arctic spring blooms (Vader et al. 2014). Their occurrence in Arctic waters during the Polar Night period has been detected by using PCR screening on both DNA and RNA indicating that *M. pusilla* and *P. pouchetii* are widely distributed in Svalbard fjords and open waters during the Polar Night. This includes ice-covered and ice-free locations, shallow and deep water and different water masses including Atlantic, Arctic and coastal water masses (Vader et al. 2015).

Furthermore, despite their ability to form resting spores, diatoms are also well known for being able to survive extended periods in a vegetative state without light, spanning from several months to years (Palmisano and Sullivan 1983; Zhang et al. 1998; Veuger and van Oevelen 2011). In line with this, low abundances of vegetative diatom cells have been recorded from all studies in Svalbard waters during the Polar Night, including several *Thalassiosira* species, *Attheya septentrionalis*, *Cylindrotheca closterium*, and *Pleurosigma cf. stuxbergii* (Brown et al. 2015; Kvernvik et al. 2018). In deeper water layers and in the sediment surface layer, Brown et al. (2015) found even more, mostly pennate diatom species, including several that are found in sea ice during spring, such as *Nitzschia frigida*, *Entemoneis* sp., and *Navicula transitans* – but also centric diatoms of the genus *Chaetoceros*. More details about their physiological state and survival strategies are described in section 4.5.1.

4.3.2 Microphytobenthos

Microphytobenthos consists of microalgae growing mainly on top of intertidal and neritic benthic habitats. Communities consist of eukaryotic unicellular algae plus cyanobacteria and in the Arctic are often dominated by pennate diatoms (Smola et al. 2015), similar to the ice algae (see below). Although often ignored, they play a significant role in global primary productivity and may contribute 20% of the global marine primary production (Cahoon 1999). However, their significance in Arctic marine waters has rarely been studied.

The likely most detailed Arctic study was conducted in the high Arctic Young Sound, in Greenland by Danish scientists (Glud et al. 2002). For this shallow nearshore ecosystem they determined that total annual marine primary production originated to 40% from the diatom dominated microalgal mats, while 60% came from kelp. Similar astonishing high fractions of microphytobenthos contributions to total primary production were also reported from other parts of the Arctic, including the Chukchi Sea, Beaufort Sea and Barents Sea (reviewed in Glud et al. 2009). In these studies, contribution to microphytobenthos to total production ranged from 0 to 30% with strong seasonal variations. These microalgal communities can be species rich as reported from other northern study sites like e.g. Iceland, where Scholz and Einarsson (2015)

observed 137 different microalgal species, dominated by diatoms (with 106 taxa). Non diatoms in the microalgal mats include typically phototrophic but also heterotrophic representatives of cryptophytes, dinophytes, haptophytes and euglenophytes. For Svalbard waters, a study by Woelfel et al. (2010) estimated similar productivity rates for microphytobenthos and phytoplankton for Kongsfjorden. The high productivity of microphytobenthos can be explained by a) high exposure to light in the intertidal range and b) additional nutrient supply through the sediment remineralization processes below (Glud et al. 2009).

Certain adaptations allow the benthic microalgae to survive under the harsh local environmental conditions. Unique to intertidal habitats, motility (e.g. by flagellated taxa and raphid diatoms) reduces exposure to freezing air temperatures or ice gouging in winter or in summer full solar exposure during low tide. Formation of aggregates and large amounts of released extracellular material (Goto et al. 2001) glues cells to substrates reducing the risk of being washed away by wave action.

The dark season can be survived based on stored energy in form of lipid droplets as demonstrated for the benthic diatom *Navicula perminuta* from Svalbard Adventsfjorden (Schaub et al. 2017). Some microalgal mats have been reported far deeper than the intertidal zone at great water depths down to 245m from the Barents Sea (Druzhkova et al. 2017) with however lower abundances and reduced species diversity compared to the nearshore littoral assemblages. The high potential of microphytobenthos survival of dark periods has even been demonstrated from non-Polar regions (Wadden Sea, Veuger and van Oevelen 2011), where living, Chl a containing diatom cells were found even after one year of incubation in complete darkness using a mixture of strategies including resting spores, reduced metabolism or a shift towards mixotrophic nutrition. It has also been suggested that cold water temperatures allow for longer dark period survival. Thus, sediments at the end of winter do not only harbor the resting spores for reseeded part of the phytoplankton bloom, but also its own communities of microalgae, adapted to live in intertidal and sublittoral areas throughout the year.

4.3.3 Sea ice algae

Sea ice provides a unique habitat for algal growth in the Arctic (Bluhm and Gradinger 2008), although its characteristics can be challenging (Fig. 4.1). Growth conditions include reduced light intensity, vast temperature and salinity gradients and reduced nutrient availability compared to the water column. At the same time, sea ice algae are relatively well protected against grazing, and will not get mixed far down in the water column where light availability is insufficient for photosynthesis. Sea ice algae in Arctic waters contribute significantly to total primary production and algal diversity, although their share of annual production is very variable, and ranges from about 2 to more than 50%. Due to their adaptation to extremely low light intensities and their stable habitat that prevents them from vertical mixing, they are usually the first ones to start growing in spring upon the return of the sun. Thereby, they extend the productive season in high latitudinal ice-covered waters substantially. It is the ice algal bloom that marks the winter–spring transition in high latitude systems, as phytoplankton typically start blooming only after the sea ice has reached an advanced state of melt and disintegration (reviewed by Leu et al. 2015; Assmy et al. 2017; Kauko et al. 2017, 2018; Olsen et al. 2017). It is not well known how ice algae overwinter in the Arctic and are able to bloom the following spring. In coastal areas, they might get re-suspended from sediments during water column turnover in winter time. In a seasonal study of the pack ice north of Svalbard between January and June 2015, scientists found that multiyear ice can function as a seed repository for ice algae and secure a sufficient seed stock for the spring ice algae bloom (Olsen et al. 2017). During the last decades a change in the ice regime of the Arctic Ocean has been observed where multiyear ice is disappearing fast and ice-free summers could be a reality within this century. This could

compromise the seeding mechanism, in particular in the deeper central Arctic ocean, and lead to profound changes in the ice algal species composition and primary productivity.

The seeding of the sea ice happens during ice formation where ice crystals and platelets act as “sieves”, accumulating selectively species that are present in the surface water during sea ice formation (Syvertsen 1991; Gradinger and Ikaevalko 1998; Leu et al. 2011, 2015; Kauko et al. 2018; Olsen et al. 2018). Gradinger and Ikaevalko (1998) and Rozanska et al. (2008) showed that this process is size- and taxon selective and leads to a concentration of larger cells in the newly formed ice compared to the size distribution of microalgae in the underlying water. Initially, microalgae and other protist communities are rather similar between sea ice and water, but develop gradually into assemblages that differ increasingly from those in the underlying water masses. So, linked to the seasonal increase of the ice algae within the ice occurs a shift in species composition, often dominated by large pennate colony forming diatoms (Hsiao 1992). This selection process is mainly driven by the strong gradients in environmental properties within the ice, being pronouncedly different from the water column. While microalgae initially are distributed rather equally in Arctic sea ice, they accumulate over time in the lowermost part of the sea ice, close to the ice-water interface. This is both due to more favorable conditions with respect to sea ice structure and nutrient supply. Early in the season, sea ice is usually warmest in its lowest parts favoring a larger fraction of the sea ice being filled with the liquid brine channel systems which is the true habitat of sea ice algae. Also, the lowest parts of the sea ice are in direct contact with the underlying surface waters and experience from there a continuous re-supply of inorganic nutrients and carbon (Gradinger 2009). As described in Rozanska et al. (2008), the initial community composition of sea ice algae is dependent on the surface water community present during the time of sea ice formation which in that study occurred between September and November 2003 in the Canadian Arctic. Around Svalbard, however, sea ice formation nowadays starts much later, usually only towards the end of the Polar Night (late January-February), as the highest water temperatures in the fjords in western Spitsbergen are found between September and November (Cottier, Leu et al. unpublished data; Olsen et al. 2017; Kauko et al. 2018), and high positive anomalies of atmospheric temperatures during mid-winter have become rather the rule than the exception during the past winters (Isaksen et al. 2016; Chapter 2).

The Polar Night period has been described by Leu et al. (2015) as the heterotrophic phase in the life cycle. Only few studies looked at ice communities in winter time. Those reported low abundances, varying diversity and no primary productivity (e.g. Werner et al. 2007; Druzhkov et al. 2001; Gradinger et al. 2009; Riedel et al. 2008; Niemi et al. 2011). Interestingly, Niemi et al. (2011) observed no reduced diversity in winter time within the ice. Survival during winter can occur in the form of physiological or morphological resting stages (e.g. Zhang et al. 1998; Horner and Alexander 1972) with reduced activity as well as through mixotrophic nutrition including e.g. osmotrophy (detailed in 4.5.1).

The lack of sea ice during most of the Polar Night period in western Svalbard has several implications: In this region, sea ice is not any more a substrate/refuge for microalgal cells to overwinter in a state of reduced metabolic activity, while staying safe from grazer pressure in surroundings that are very favourable with respect to the return of the sun in spring (as close to the surface as possible). At the same time, the absence of sea ice (and snow cover on top) also changes the underwater light conditions and increases the occurrence of wind-induced mixing events. Although the limited irradiances that are found during the Polar Night are not sufficient for photosynthesis, even at the water surface, other light-driven ecological phenomena, such as diel vertical migration (DVM) in zooplankton continues also in open waters during the Polar Night (Berge et al. 2009; Chapter 5) and can be influenced by moonlight (Cohen et al. 2015; Last et al. 2016; Ludvigsen et al. 2018). This is relevant with respect to the grazing pressure the algal cells are exposed to during this vulnerable period.

4.4 Macroalgae

Contrary to the pronounced seasonal succession of different microalgal species with distinct bloom phases, macroalgae have a different seasonal growth pattern characterized by changes between annual and perennial species, complex life cycles, timing of reproduction and seasonal differences in growth (Fig. 4.1). In addition to the key environmental variables (4.2), the macroalgal species diversity and eco-physiology is regulated by biotic variables detailed in 4.4.1. In addition, the macroalgal species and pigment-group diversity comprises different habitats which are described in section 4.4.3 and are highly affected by seasonal changes (4.4.2) in environmental variables. In section 4.5 we discuss how two species of brown macroalgae with contrasting adaptations utilize the Polar Night for growth and development.

Compared to macroalgal regions with high species diversity, such as Southern Australia with 1155 species (Womersley 1991), Antarctica has only 119 species (Wiencke and Clayton 2002) and the Arctic \approx 150 species (Wilce 1994), of which around 80 species have been recorded from the Svalbard region (Weslawski et al. 1993, 2011). 90% of the species in the Arctic originate from Atlantic populations (Dunton 1992), especially in regions with strong influx of Atlantic waters such as Svalbard.

There is little systematic information about species distribution of macroalgae during the Polar Night in the Arctic, including Svalbard. Diving-based data collection in Kongsfjorden during summer months totaled 76 species of annual and perennial macroalgae (Hop et al. 2012, 2016; Fredriksen et al. 2014) mainly consisting of brown algae, followed by red- and green algae. By using single- and multibeam echo sounders in the same area and summer period, Kruss et al. (2017) provided biomass estimates and distribution patterns of the most important macroalgae in Kongsfjorden showing 39% macroalgal coverage (1.09 km²) of investigated areas.

4.4.1 Biological variables affecting macroalgae

In addition to abiotic key environmental variables (4.2), the biotic variables related to macroalgae biodiversity and eco-physiology include (1) Competition for light, nutrients, substrate and space (Box 4.1-2), (2) Epi-growth (Box 4.2), (3) Grazers (Box 4.3), (4) Reproduction and life cycles (Box 4.4), and (5) Polar Night survival (Box 4.5).

The major and primary biotic factors regulating the succession of macroalgal biomass, biodiversity and photosynthetic performance is **competition for light, nutrients, substrate and space** (see section 4.4, Box 4.1-2 and 5). The high biomass and diversity of perennial macroalgae are most probably due to their “Polar Night mode” utilizing high winter-concentrations of nitrate and phosphate in winter time to grow based on stored energy (ATP and sugar compounds) synthesized during summer months through photosynthesis (Fig. 4.1A; Wiencke et al. 2007; Scheschonk et al. 2019). Some kelp species ability to grow during winter darkness/at extreme low irradiances may also be another adaptation to Polar Night and low light conditions, also detected in several kelp species in coastal Norway during winter time (Valle 2004; Forbord 2004; Hilstad 2005; Fig 4.1A, Fig 4.5).

Epi-growth on larger species of macroalgae, reflects the competition for light and substrate (Box 4.2). The species diversity of epifauna on *Saccharina latissima* were similar for stones and holdfasts and was higher during Polar Night relative to spring and autumn (Shuntanova et al. 2018). Epifauna species richness and abundance demonstrated a clear tendency to increase in accordance with substrate stability. Data on seasonal changes in sessile epifauna at high latitudes are sparse since winter sampling under Arctic condition is logistically difficult (Berge et al 2015b; Shuntanova et al. 2018). Epigrowth on lamina, stipes and hapter

of *Laminaria solidungula* is low relative to larger kelp species and may be a result of living in “the shade” under the canopy of larger kelp species (unpublished results, Fig 4.5B).

In Svalbard waters, there are few species that can be defined as macroalgal grazers (Box 4.3). As far as we know, there are no fish species in this region that feed on living algae, contrary to the large numbers of macroalgal grazing fishes in tropical regions such as Hawaii and Great Barrier Reef in Australia. The major grazers that are found in Svalbard during the Polar Night are the urchin *Strongylocentrotus droebachiensis* and the snail *Margarites* spp. (Box 4.3). A study of palatability using 19 abundant macroalgal species from Spitsbergen showed that most species were at least moderately palatable to a sympatric amphipod (*Gammarellus homari*) and *S. droebachiensis* (Wessels et al. 2006). The ecological relevance of macroalgal detritus and food-web subsidies along an Arctic fjord depth-gradient are described in Renaud et al. (2015, see Chapter 6).

How the light climate regulates the annual cycles for macroalgal reproduction (Box 4.4; Wiencke et al. 2007) is largely unknown. What we do know is that especially the photo-period is the major cue for regulation of the development of gameto- and sporophytes of macroalgae. In section 4.4.2 we describe how some species of kelp survive the Polar Night. In addition, the function of kelp forest as a habitat to find food and shelter for fish and other inhabitants are greatly unknown. Lastly, new observations (Johnson, unpublished) of deep water fish in shallow part of kelp forests during the Polar Night indicate another knowledge gap that needs to be examined, especially related to indirect (e.g. climate changes) and direct anthropogenic disturbances (e.g. habitat destruction or oil spills, Chapter 7 and 10).

4.4.2 Seasonal changes in phaeophytes, rhodophytes and chlorophytes

The macroalgal biomass is dominated by brown algae (phaeophytes) during the Polar Night, especially the larger kelp species belonging to the genera *Laminaria*, *Saccharina*, *Alaria* and *Sacchoriza* (Fig 4.2). Only one wrack species is common in Svalbard and is also found during winter time, the perennial *Fucus distichus*. This species is often seen along shorelines with little sea-ice scouring at all seasons (Fig 4.2, Box 4.1). Based on SCUBA diving surveys in the Kongsfjord area in January 2010-2017, the dominating and shallowest living kelp species of brown algae is the species complex *Saccharina nigripes/Laminaria digitata* (Lund et al, in prep; Fig 4.3A).

Correspondingly, the turbid waters in spring and summer will obtain a greenish hue reducing the efficiency of photosynthetic pigment absorption in the blue and red part of the visible spectrum, thus reducing the light utilization in brown and green algae favouring the green light absorbing specialists such as phycobiliprotein-containing red algae (Fig. 4.3). During the summer-time, the fresh water run-off will contribute to a significant **sedimentation** that also may cause embedding of macroalgae, sometimes changing the bottom substrate in inner parts of the Svalbard fjords (Fig 4.2). During summer time a significant nutrient limitation is evident (Leu et al. 2015), in contrast to the Polar Night, with ample **nutrient conditions** for macroalgal growth due to extremely low biomass of non-photosynthesizing phytoplankton and renewal of nutrients from deeper waters (winter mixing).

Due to the **recent loss of sea-ice scouring** as a consequence of warmer climate (Chapter 2) such as in western Svalbard fjords, the barren zone of perennial species (often observed before 1998; own annual observations 1987-2018), typically from 0-3 m depth, are now habitats for several species of kelp (discussed in 4.4.3; Bartsch et al. 2016). Usually below the zone dominated by the *S. nigripes/Laminaria digitata*-species complex, *Saccharina latissima* dominates in regions with low wave exposure, especially in fjord systems. Inbetween these large kelp species *L. solidungula* is typically found beneath the canopy and may be hard to

detect (Fig 4.2-3 and 4.5). In the same zone we also find patches of *Sacchoriza dermatodea* and very often high biomass of *Alaria esculenta*. Usually, quite dense kelp forest dominated by *A. esculenta* are found from 10-30 m depth in areas with good water visibility (Fig 4.2-3).

Many of the red and green algae are annual and not detected during the Polar Night. This is mainly a consequence of low light conditions and presence/absence of ice-scouring in shallow areas (Box 4.1). In addition, the rather complex life cycle of all macroalgae, which can involve microscopic generations attached to hard substrates is not easily detectable. Of rhodophytes, all calcareous red algal species are perennial and therefore found during winter time, but to our knowledge there are no reports on their biology during Polar Night (Fig. 4.3). Of leafy species of red algae, both old and new (apparently new tissue) specimens of *Palmaria palmata* have been observed during Polar Night in January in W-Spitsbergen (Box 4.5). The remaining red algae found during winter-time, eg. *Dumontia contorta*, *Devaleraea ramentacea*, *Polysiphonia arctica*, *Ptilota gunneri* and *Odonthalia dentata* appeared of old and often partly degraded tissue (unpublished observations). In the eu-littoral zone, the red algal species (of family Palmariceae) *Devaleraea ramentacea* (earlier called *Halosaccion* or *Fucus ramentaceum*) and *Palmaria palmata* (often epiphytic on kelp) are the most prominent species and easiest to find at low tide or by SCUBA diving. Important epigrowth host species for red algae are the kelp genera *Laminaria*, *Saccharina* and *Alaria*. Characteristic for the lower sublittoral are the red algae *Phycodrys rubens* and *Ptilota gunneri* and coralline red algae.

Only a few green algal species have been observed during the Polar Night by means of SCUBA diving. *Ulva*-like (sea salad) specimens have been observed regularly (*Monostroma* spp, *Ulvaria* sp.) both in bad condition, but also specimens that look fresh and viable have been seen. *Chaetomorpha melagonium* has quite regularly been observed attached to hapter of major kelp species in good condition during January in Kongsfjorden 2010-2017. The hapter of kelp is typical habitat for this species at all seasons. Green algae (leafy and thread forms) are typically found in the upper eu-littoral zone and in and close to freshwater outlets such as river banks. The latter is due to the chlorophytes typical ability to cope with low salinities, compared to rhodo- and phaeophytes. Some decades back, green algal growth in river outlets was thought to be an indication of nutrient eutrophication. But, looking at small and larger river outlets, with low concentration of N and P in Svalbard, these regions are often dominated by green algae that are active osmotic regulators and can cope with rapid changes in salinity (unpublished data). Species such as *Monostroma* spp, *Acrosiphonia arcta*, *Enteromorpha*, *Ulvaria* spp, *Cladophora*, *Urospora*, *Ulotrix* are typically found from 0-4 m depth, often as green biofilm on rocks (splash zone) and in sandy substrates with rock from 0-2 m depth (unpublished data). Due to climate changes, a higher fresh water run-off during winter time are likely and may change the bio-diversity and biomass of low salinity tolerant and shallow leaving green algae in Svalbard.

4.4.3 Habitats for perennial macroalgae

Rocky shores along the west, north, east and south coasts of Svalbard are the major habitats for brown-, red- and green macroalgae. The **littoral zone** is divided into eu-littoral (0-3 m), mid-littoral (3-10 m) and sub-littoral zone (10-60 m, Fig. 4.2). **Competition for space**, finding available substrate, is often the limiting factor for macroalgae and may result in well-developed epialgal growth (epigrowth) where smaller species/specimens grow on larger algae, which is also reflected in **no distinct vertical zonation** between algal species or pigment groups (Box 4.2). In contrast, a distinct macroalgal zonation pattern is highly evident along the Norwegian coast and rest of Europe.

Further, during the Polar Night including spring, **ice-scouring** from sea ice has been one of the environmental variables causing the kelp forest to start at 3-5 m depth enhancing resource competition between species and reducing zonation patterns in the mid-littoral zone. Sites that are exposed to waves and sea-ice scouring do have completely different algal assemblages compared to sheltered areas (Fig 4.2). The kelp forest foundation species, usually found at 3-15 m depth, are currently found some places at surface at low tide, due to warmer surface waters along Svalbard since 1998 caused by reduced abrasion of macroalgae due to ice-scouring. After 1998 the upper growing zone of kelp is surface (splash zone) in areas with little sea-ice and new, more shallow growing kelp forest habitats are emerging (own bi-annual observations in May from 1996-2018 and in January from 2010-2017 in Kongsjorden). These shallow water kelp forest zones induce a possibly higher marine primary production and a larger vertical macroalgal growth zone along the coast with additional effects on associated fauna and algae (Bartsch et al. 2016; Scheschonk et al. 2019). Ice-scouring, especially during the winter-spring period, may cause rapid changes in community structure (Box 4.1; Fig. 4.2; Volent et al. 2007). Regions that are heavily affected by ice-scouring, such as Rossøya (80.82890°N, 20.35002°E, the northernmost island of “Sjuøyane” in the Svalbard archipelago, is characterized with barren areas from the surface to 2-3 meters water depth and with only annual species found, except in regions sheltered from ice scouring, such as the perennial wrack *Fucus distichus* in cracks in between bedrock or in spaces between larger rocks (Box 4.1, Fig. 4.2). At this site, we also find a kelp forest dominated of *Alaria esculenta* down to 30 m depth and the specimens at this site are characterized by thin and transparent lamina, probably due to adaptation to the extreme low irradiances at this depth where sea-ice, until two decades ago, covered the sea surface most of the year (Fig. 4.2).

Brown algal habitats in the upper eu-littoral (splash zone to mid-littoral) along Spitsbergen in summer are often dominated by the brown algae *Fucus distichus*, *Pylaiella littoralis* and *Chordaria flagelliformis*, with the two latter species, to our knowledge, being not observed during the Polar Night (Fig. 4.2). The Arctic kelp *L. solidungula* occurs often in the lower sub littoral zone around the Svalbard archipelago (own observations, Belseth 2012), but has been often found at 2-5 depth and then as a shade algae under the large kelp species canopy zone (Fig. 4.5). *Laminaria solidungula* can also be found in the inner part of the fjords (Bartsch et al. 2016), but also in current rich straits such as Hinlopenstredet (Belseth 2012; Fig 4.5).

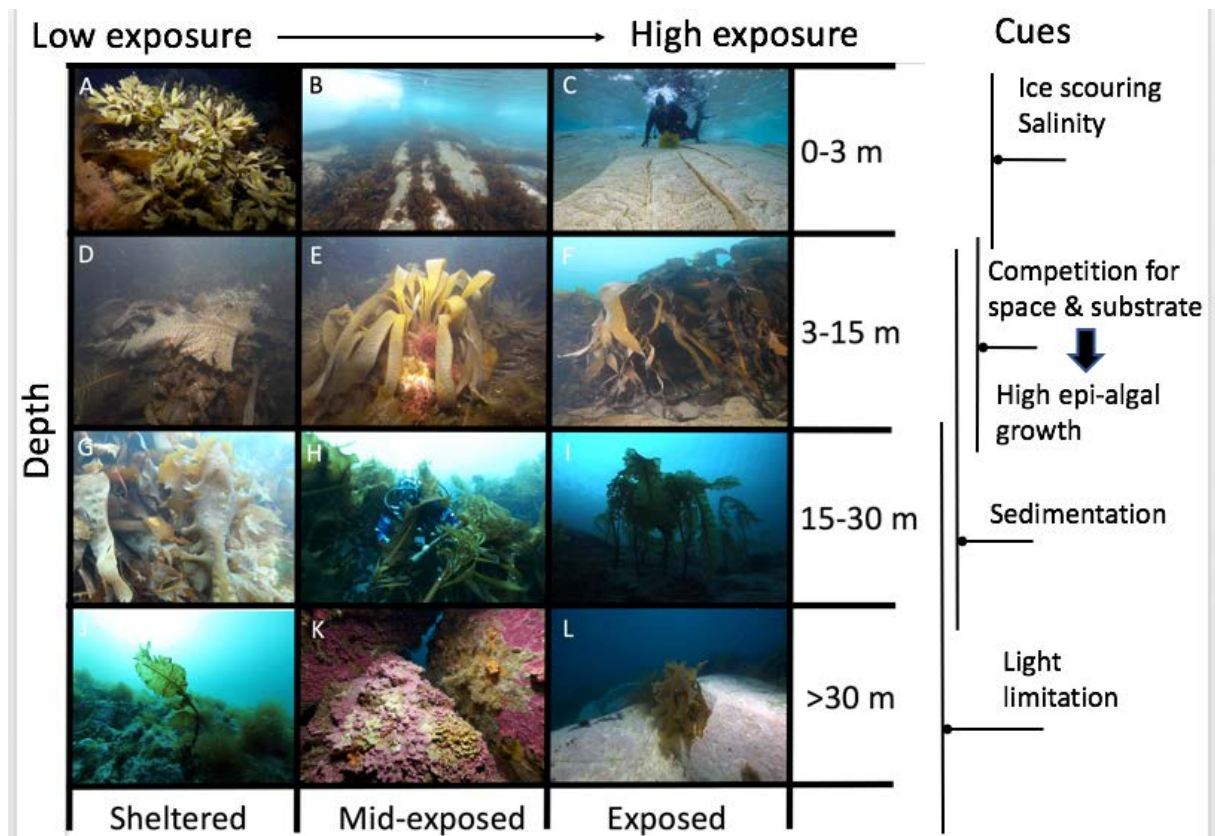


Fig 4.2. Svalbard kelp forest dominated by perennial brown algae as a function of habitat exposure (X-axis) and depth (Y-axis, 0-30 m depth).

Exposure: Low exposure (sheltered habitat, mid Kongsfjord): A. *Fucus distichus* and *Chordaria flagelliformis* at surface, no ice-scouring (Sep), D. *Alaria esculenta* with sediments (Sep), G. *Saccharina latissima* dominating (typical for sheltered regions), with *Laminaria solidungula* in middle (shade algae), green and red algae also present (Sep). J. *Alaria esculenta* and *Desmarestia aculeata* are often the two remaining brown algae species at 30 m depth (Sep). If high urchin grazing pressure at this depth, the remaining brown algal species are often the sulfuric-acid containing *Desmarestia aculeata*, which seems not to be preferred by urchins. Deeper than 30 m is dominated by red coralline algae (see K and L). **Mid-exposed** habitat (northern Hinlopenstredet): B. Ice-scouring affecting presence of *Laminaria digitata/Saccharina nigripes*, *Fucus distichus* and red coralline algae (Sep), E. *Saccorhiza dermatodea* and red alga *Dumontia contorta* (Sep). H. Kelp forest dominated by *A. esculenta* >15 m depth (Sep), K. Red coralline algae on shadow-zone of larger rocks (Sep).

Exposed habitat (northern Rossøya): C. Ice-scoured rock from 0-3 m depth, with small annual species of macroalgae in cracks (Sep). F. Thick kelp forest starting at 4 m depth dominated by *S. nigripes/L. digitata* and *A. esculenta* (Aug). I. *Alaria esculenta*, is the dominant brown algae at 30 m depth. L. At depths >30 m, the last *A. esculenta* are seen and the macroalgal communities are dominated by red coralline algae.

Depth: A-C: Eu-littoral zone (0-3 m) with low exposure to left and high exposure and ice scouring to the right. D-F: Mid littoral zone (3-15 m) with low exposure and affected by freshwater run-off with sediments to the left and high wave- and current exposure to the right. G-I: Sub littoral zone (15-30 m). Sheltered kelp forest dominated by *S. latissima* and exposed kelp forest dominated by *A. esculenta* at Rossøya. J-L: Light limited zone: (>30m), kelp forest species few to absent and dominated by red coralline algae. Photos: Geir Johnsen.

Habitats dominated by calcareous algae can be divided into three growth forms and type 1-2 are most prominent in waters around Svalbard (review by McCoy and Kamenos 2015):

1. **Rhodolith or “maerl” seascape** comprising of loose fragments of calcareous matter (1-100 cm in size) provide an important hard substrate habitat for colonization by other marine algae and invertebrates (Fig 4.3C). 2. **Crustose calcareous algal layer** or “carpet”, growing on bedrock and larger rocks (Fig 4.3A-B). 3. **Articulated growth forms** (algal frond growing from a basal crust), this growth form is the least prominent of the three different coralline growth forms in Svalbard waters.

The type 1 and 2 (Fig 4.3) of red calcareous algae are called non-geniculate growth forms in contrast to the articulated red calcareous algae (type 3) for geniculate growth forms. Many arctic non-geniculate corallines, inhabiting the intertidal or subtidal depend on shading by the macro-algal kelp canopy, are competing for light and holdfast space. Type 1-2 red algae are also be found in extreme low-light areas down to 80 m depth and underside of kelp canopies, rocks and in caves (Fig 4.3). Coralline algae live in varying water depths, ranging from periodically exposed intertidal settings to 270 m water depth (around the maximum penetration of light, Aguirre et al. 2000). The red calcareous algae produce an array of secondary metabolites such as halogenated bromides thought to reduce palatability, digestibility, or nutrition of algal tissue. Some of the coralline algae inhibit settlement of barnacles, filamentous diatoms and other macroalgal species. Many invertebrates such as shrimps, brittle stars, mussels, urchins, anemones and polychaetae’s live on/inside rhodoliths or burrow in surrounding sediments (Fig 4.3). A high areal cover of non-geniculate coralline algae is typically easily detectable due to absence of kelp cover caused by grazing of urchins, in shallow areas at 2-5 depth or in areas beneath kelp canopy at depth >5 m (Box 4.3).

Coralline algae are important carbonate producers and the high latitude habitats have so far received little attention compared to warm-water coralline algal beds in this context, except a comprehensive study from Greenland (Jørgensbye and Halfar 2017). High latitude branched non-geniculate species can have low growth rates as low as 200–300 $\mu\text{m year}^{-1}$ (McCoy and Kamenos 2015), related to lower irradiance and colder water temperatures at high latitudes. Generally, temperate non-geniculate coralline algae are low-light adapted (Burdett et al. 2012), and exposure to higher irradiances causes a reduction in photosynthetic activity and bleaching of algal tissue, related to loss of photosynthetic pigments in surface cells (Irving et al. 2004; Martone et al. 2010). Both rhodolith beds and coralline carpets are important in the coastal carbon cycle in temperate areas. Carbonate accretion rates, attributable to red coralline algae, can vary between 79 and 1432 $\text{g CaCO}_3 \text{ m}^2 \text{ year}^{-1}$ in North Atlantic rhodolith beds (Bosence 1980; Freiwald and Henrich 1994).

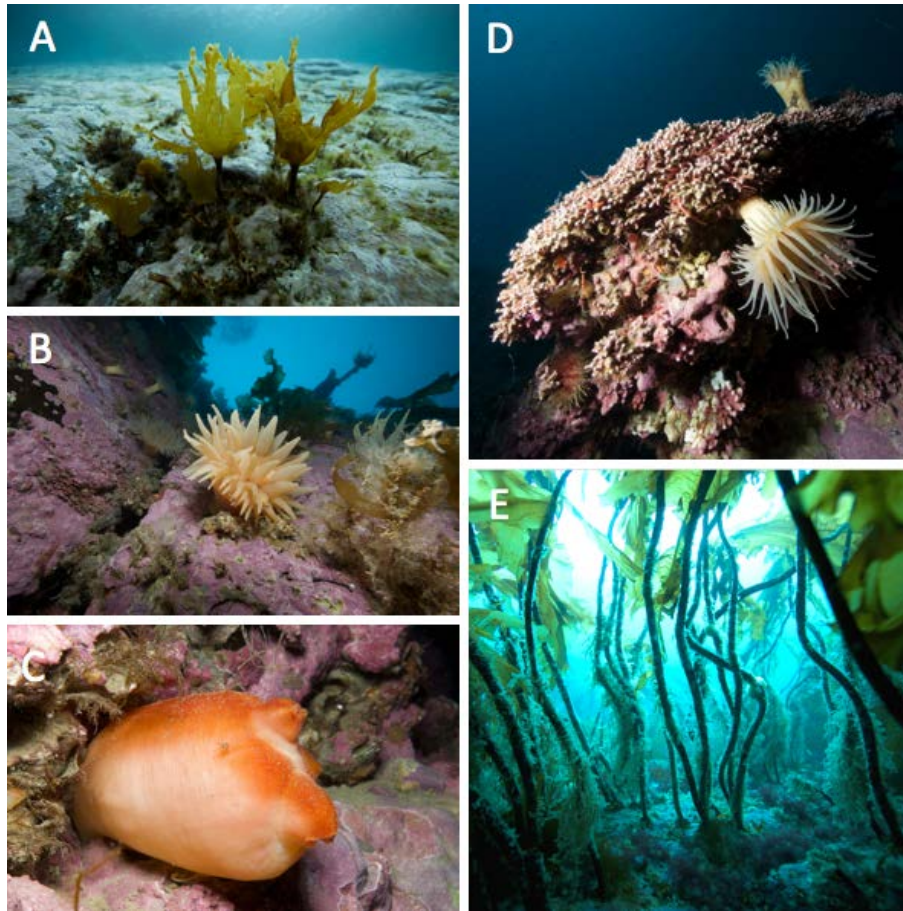


Fig 4.3. Red calcareous algae habitats. A. Typical crustose eu-littoral seascape (type 2 habitat by red calcareous algae) with shallow growing *Saccharina nigripes*. Picture from Tommelen, 4 m depth, Hinlopenstredet. B. Large areas covered by crustose red calcareous algae, creating seascape substrate for several benthic organisms such as anemones and hydroids. This type of habitat is found at exposed seafloor and vertical walls below kelp forest (>15 m depth). From 25 m depth, Hinlopen strait. C. Rhodoliths, creating “Mearl seascape” comprises loose fragments of red calcareous algae providing fasthold for several benthic organisms such as tunicates, often dominated by the orange tunicate *Halocynthia pyriformis* and shrimps (two of them on tunicate). Photo from Sagaskjæret, 17 m depth, Isfjorden. D: Combination of rhodolith and crustose seascape, provides habitat for numerous brittle stars, urchins (*Strongylocentrotus droebachiensis*), shrimps and anemones (*Hormathia nodosa*). Rjipfjorden, Nordaustlandet. E: Under the thick kelp canopy, the seafloor is covered by shade adapted coralline algae. Ryke Yse island, E-Svalbard. Photos: Geir Johnsen.

4.5 Ecophysiology of algae in the Polar Night

There are some fundamental differences in the environmental exposure between micro- and macroalgae. During summertime, macroalgae compete for light with suspended phytoplankton and sediments, have limited substrate for growth and algae are further affected by low salinity and reduced access to nutrients. In contrast, microalgae are mainly struggling to absorb available light and nutrients due to deep vertical mixing and nutrient depletion and are also heavily grazed upon by zooplankton. During the Polar Night, the photosynthetic (autotrophic) microalgae are basically in a resting or a “heterotrophic” mode (Fig. 4.1; Fig 4.4), while some kelp species are actually using Polar Night darkness to grow (Section 4.5.2; Fig 4.5B), using stored laminaran in the lamina synthesized during the well-lit summertime (Wiencke et al 2007; Wiencke 2011; Scheschonk et al. 2019).

4.5.1. Microalgae: Different survival mechanisms, but ready anytime

Different groups of microalgae have developed various strategies to cope with the lack of light, preventing photosynthetic activity (Table 4.2). In sea ice and in the water column a predominance of small species is found, with a high contribution of mixotrophic and heterotrophic species (Niemi et al. 2010; Marquardt et al. 2016). Heterotrophy describes the ability of living on organic particulate or dissolved C, while mixotrophic organisms are able to perform photosynthesis if light is available, but can switch to different heterotrophic strategies in the dark. They either obtain organic C in a phagotrophic mode digesting POC (particulate organic matter, such as feeding on bacteria or organelles from eukaryotic phytoplankton) or they rely on osmotrophy by taking up DOC (dissolved organic matter, see review of Stoecker and Lavrentyev 2018). Stoecker and Lavrentyev (2018) suggested that mixotrophy may be an adaptation to Polar Night to survive the extreme annual variation in solar irradiance. They highlighted several species belonging to mixotrophic flagellates such as *Micromonas* and *Pyramimonas* (prasinophytes), *Dinobryon* (Chrysophyte), cryptophytes, prymnesiophytes and dinoflagellates also found in the Svalbard area (Iversen and Seuthe 2011; Seuthe et al. 2011; Johnsen et al. 1999, 2018).

Interestingly enough, the likely most abundant Arctic eukaryotic phytoplankton species *Micromonas pusilla* is capable of mixotrophy by ingesting bacteria as alternative organic carbon and nitrogen source (McKie-Krisberg and Sanders 2014). A mixotrophic lifestyle is not only restrained to microalgae but is also an important trait for unicellular ciliates. Stoecker and Lavrentyev (2018) state that the key Arctic copepod species preferred to feed on chloroplast-bearing ciliates forming an important link in the planktonic food web. Further, knowledge of initiation and interaction between microalgae and ciliates with respect to algal colonization of sea-ice is not well elucidated. Kauko et al. (2018) described algal colonization of young Arctic sea ice at 82°N (Yermak Plateau, N of Svalbard) showing a highly dynamic succession starting in first week of May with the ciliate *Mesodinium rubrum* containing cryptophyte chloroplasts, followed by dinoflagellates and then ending the succession with 90% of total biomass comprising diatoms in early June. Stoecker and Lavrentyev (2018) highlight that mixotrophic plankton persist in the water column during the Polar Night when irradiance is extremely low suggesting that at high latitudes an alternative food web based on mixotrophy may dominate the pelagic lower food web during much of the year (Table 4.2).

During a field sampling campaign in Kongsfjorden in January, we collected algae samples from both surface waters, but also sediments. Microscopic analyses of live specimens revealed a strong Chl a fluorescence, suggesting a healthy physiological state of these specimens (Fig. 4.4, Leu et al., unpublished data). Here, resuspension from sediment appears

to be an important pathway to reestablish algal populations for the spring bloom due to early spring storms.

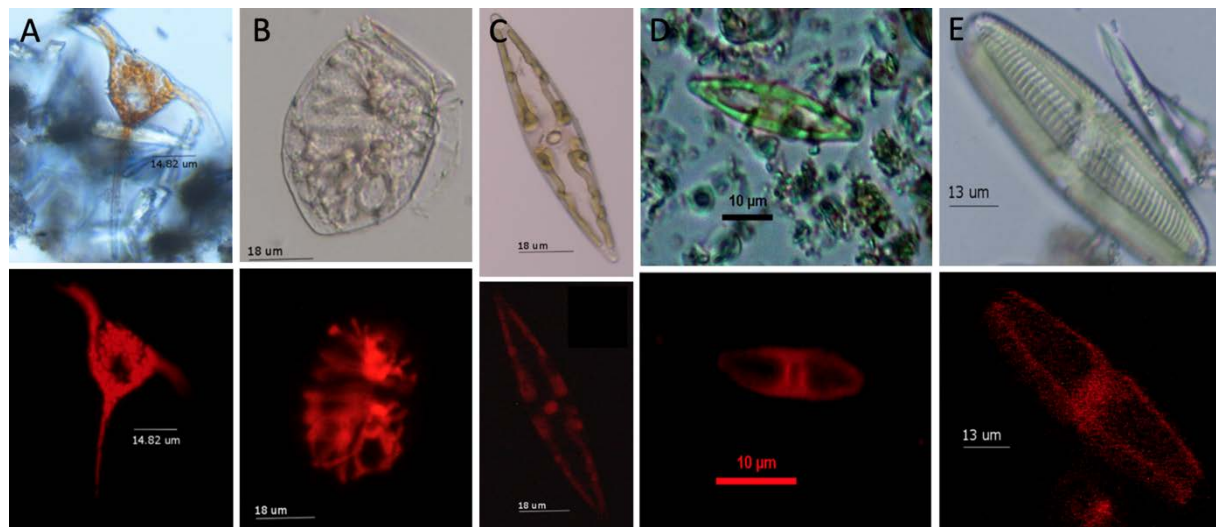


Fig 4.4. Light micrographs of microalgae collected January 2015 in Kongsfjorden. Upper panel: White light images. Lower panel, the corresponding *in vivo* Chl a fluorescence images. Phytoplankton from surface waters: A. *Ceratium arcticum*, B. *Dinophysis* sp. and C. *Pleurosigma* cf. *stuxbergii*. Pennate diatoms from sediment surface samples (about 300 m depth): D. *Navicula transistans* and E. *Trachyneis aspera*. Photos: Zofia Smola

For microphytobenthos, Schaub et al. (2017) showed that benthic diatoms survived the Polar Night by metabolizing their lipid reserves. The rate at which they utilized their lipid reserves was temperature-dependent and increased at higher temperatures as a consequence of higher metabolic rates. This supports the general statement that colder temperatures allow for longer dark survival of microphytobenthos (see above).

Hardly any studies of detailed physiological processes of natural phytoplankton communities during the Polar Night have been carried out so far. But Kvernvik et al. (2018) demonstrated through *in situ* measurements of photosynthetic carbon fixation in concentrated natural phytoplankton communities in surface waters during the Polar Night that there is no measurable primary production under ambient conditions. However, when collecting samples of these communities and exposing them to light, a very rapid re-activation of photosynthetic activity can be observed within hours. Physiological characteristics of these algae after 24 hours of re-illumination are very similar to those measured during an ordinary spring bloom in April/May in these areas (Kvernvik et al. 2018). A similarly rapid response of increased growth to light exposure was demonstrated for ice algal cultures maintained for months in complete darkness (Zhang et al. 1998). For sea ice algae, Manes and Gradinger (2009) observed low photosynthetic performance measured as quantum yield of Chl a fluorescence from PSII (Φ_{PSII}) and relative ETR_{max} (maximum electron transfer rate) for PSII (photosystem II) when comparing December to March for fast ice samples from Barrow, Alaska. Interestingly, similar delay of algal growth cannot only be caused by the Polar Night, but also due to substantial sediment load in Arctic sea ice (Gradinger et al. 2009). In addition to use of stored lipid reserves, osmotrophy has been proven for some Arctic sea ice diatoms by Horner and Alexander (1972). Long survival under dark conditions was also shown for Antarctic sea ice diatoms (Bunt and Lee 1972). While diatoms are limited in their ability to ingest particles due to their diatom frustules, ingestion of particles (e.g. bacteria, other algae) is a well-documented pathway for

pelagic microalgae (see above). A compact overview of the most important strategies found in Antarctic microalgae was compiled by McMinn and Martin (2013). An overview of algae found during the Polar Night at different habitats in Svalbard are shown in Table 4.2.

Habitat	Class	Genus/Species	Auto	Hetero	Mixo	location	Method	Ref	
Seawater	Diatoms	Pennate diatoms, indet.	x			Rijpfjorden	LM	1	
		Diatom spores				Rijpfjorden	LM	1	
		<i>Cylindrotheca closterium</i>	x			Sofiadjupet	LM	2	
		<i>Entomoneis</i> sp.	x			Sofiadjupet	LM	2	
		<i>Gyrosigma fasciola</i>	x			Rijpfjorden	LM	2	
		<i>Nitzschia</i> sp.	x			Sofiadjupet	LM	2	
		<i>Pseudonitzschia</i> sp.	x			Rijpfjorden	LM	2	
		<i>Pseudonitzschia pseudodelicatissima</i>	x			Sofiadjupet	LM	2	
		<i>Thalassiosira</i> sp.	x			Rijpfjorden, Sofiadjupet	LM	2	
		<i>Thalassiosira</i> sp. cf. <i>angulata</i>	x			Sofiadjupet	LM	2	
		Diatom spores				Sofiadjupet	LM	2	
		<i>Actinocyclus</i> sp.	x			Adventfjorden	LM	3	
		<i>Pleurosigma</i> cf. <i>stuxbergii</i>	x			Adventfjorden, Kongsfjorden	LM	3	
		<i>Thalassiosira antarctica</i>	x			Adventfjorden	LM	3	
		<i>Thalassiosira</i> sp.	x			Adventfjorden, Kongsfjorden	LM	3	
	Dinoflagellates	<i>Neoceratium arcticum</i>	x			Rijpfjorden, Sofiadjupet	LM	2	
		<i>Neoceratium fusus</i>	x			Sofiadjupet	LM	2	
		<i>Polarella glacialis</i>				Rijpfjorden	LM	1	
		Naked dinoflagellates				Rijpfjorden	LM	1	
		<i>Thecate peridinea</i>	x			Rijpfjorden	LM	2	
		<i>Torodinium robustum</i>	x			Sofiadjupet	LM	2	
		<i>Dinophysis rotundata</i>		x		Rijpfjorden	LM	2	
		<i>Gymnodinium</i> sp. cf. <i>wulfii</i>		x		Rijpfjorden, Sofiadjupet	LM	2	
		<i>Gymnodinium wulfii</i>		x		Rijpfjorden	LM	2	
		<i>Pronoctiluca pelagica</i>		x		Sofiadjupet	LM	2	
		<i>Protoperidinium cerasus</i>		x		Rijpfjorden	LM	2	
		<i>Protoperidinium pellucidum</i>		x		Sofiadjupet	LM	2	
		Gymnodiales				x	Rijpfjorden	LM	2
		<i>Gymnodinium galeatum</i>			x		Rijpfjorden, Sofiadjupet	LM	2
		<i>Gymnodinium</i> ssp.			x		Rijpfjorden, Adventfjorden	LM	2
		<i>Peridinea</i> cysts					Rijpfjorden, Sofiadjupet	LM	2
		<i>Gyrodinium helveticum</i>					Adventfjorden	DNA	4
		<i>Gyrodinium fusiforme</i>					Adventfjorden	DNA	4
<i>Glenodinium</i> sp.						Adventfjorden	DNA	4	
<i>Dinophysis</i> cf. <i>acuminata</i>						Adventfjorden	LM	3	
<i>Phalacrocoma rotundatum</i>						Kongsfjorden	LM	3	
<i>Podolampas palmipes</i>						Adventfjorden, Kongsfjorden	LM	3	
<i>Protoperidinium brevipes</i>						Adventfjorden, Kongsfjorden	LM	3	
<i>Protoperidinium</i> sp.					Kongsfjorden	LM	3		
Ciliophora	<i>Parafavella</i> sp.				Adventfjorden, Kongsfjorden	LM	3		
	<i>Tintinnida unident.</i>				Adventfjorden, Kongsfjorden	LM	3		
Dictyophytes	<i>Dictyocha speculum</i>	x			Rijpfjorden, Sofiadjupet	LM	2		
Picoflagellates	<i>Micromonas pusilla</i>				Billefjorden, Tempelfjorden, Isfjorden, Rijpfjorden, Sofiadjupet, Adventfjorden	PCR	4,5		
					Billefjorden, Tempelfjorden, Isfjorden, Rijpfjorden, Sofiadjupet	PCR	4,5		
Prymnesiophytes	<i>Phaeocystis pouchetii</i>				Sofiadjupet	PCR	4,5		
	<i>Coccolithus pelagicus</i>	x			Sofiadjupet	LM	2		
Sediment	Diatoms	<i>Porosira glacialis</i>	x			Rijpfjorden	Cult	1	
		<i>Attheya septentrionalis</i>	x			Rijpfjorden	Cult	1	
		<i>Nitzschia frigida</i>	x			Rijpfjorden	Cult	1	
		<i>Pleurosigma</i> sp.	x			Rijpfjorden	Cult	1	
		<i>Entomoneis</i> sp.	x			Rijpfjorden	Cult	1	
		<i>Navicula transitans</i>	x			Rijpfjorden	Cult	1	
		<i>Thalassiosira antarctica</i>	x			Rijpfjorden	Cult	1	
		<i>T. hyalina</i>	x			Rijpfjorden	Cult	1	
		<i>Chaetoceros furcellatus</i>	x			Rijpfjorden	Cult	1	
		<i>C. diadema</i>	x			Rijpfjorden	Cult	1	
<i>Cylindrotheca closterium</i>	x			Rijpfjorden	Cult	1			
Sea ice	Diatoms	Pennate diatoms, indet.	x			Rijpfjorden	LM	1	
		Diatom spores				Rijpfjorden	LM	1	
	Dinoflagellates	Naked dinoflagellates		x		Rijpfjorden	LM	1	

Table 4.2 Microalgal species found during the Polar Night in Svalbard. Abbreviations: 1 = Brown et al. (2013), 2 = Biachowiak-Samołyk et al. (2014), 3 = Kvernvik et al. (2018), 4 = Marquardt et al. (2016), 5 = Vader et al. (2014). Examination methods: LM = light microscope, DNA = DNA/RNA analysis, PCR = PCR screening and Cult = algal cell cultivation. Nutrient modes: Auto = autotrophic, hetero = heterotrophic and mixo = mixotrophic species.

4.5.2. Macroalgae: Season anticipators

Contrary to microalgae that struggle to secure survival during the Polar Night darkness, some macroalgal species are capable of utilizing the winter darkness or initial spring period as growth seasons. Season anticipator macroalgae are characterized with annual growth and reproduction regulated by photoperiod (daylength, see also Section 4.2; Chapter 3) and circannual rhythms, triggered or synchronized by daylength (Wiencke et al. 2007).

Apart from the darkness, the Polar Night is a period with favourable conditions in many respects for macroalgae such as **low stress with respect to osmoregulation** due to close to no fresh water run-off (frozen glaciers, dry river beds) and there is no need to spend energy to acclimate to rapid diurnal changes in salinity over 4-8 months (Oct-May). Climate warming is about to change this, and since 2009 the glaciers in Kongsfjorden have provided freshwater run-off in warm periods in January (weeks) with air temperatures up to 5°C. Also, during the Polar Night, the **sedimentation** of minerals and biogenic particles is at an annual low. Likewise, with stable temperatures at -2 to 2°C and salinity is close to 35 at all depths are favourable for macroalgae. In winter, **low seawater temperature differences over long period** is typical in surface layers (- 1.8 to 2°C) with minor differences between day and night, in contrast to summertime. The upper survival temperature (UST) and upper limit temperature for gametogenesis (ULG) limits the distribution of North Atlantic macroalgal species in the Arctic affected by lethal high summer temperatures (especially at low tide in Arctic W-Atlantic) and high winter temperatures may inhibit reproduction (Arctic E-Atlantic, Wiencke et al. 2007; Box 4.4). **High macronutrient** values during winter are beneficial for “heterotrophic” macroalgal growth in the absence of competition by microalgae. In addition to vertical mixing, the West-Spitsbergen current continuously provides high nutrient supply, especially in the western and northern part of Svalbard. This is also one major reason for the high marine production in this area of the Arctic with respect to high phytoplankton and kelp forest biomass.

Recent research has demonstrated that the Polar Night is a period of development, reproduction and maturation for different marine organisms at water surface, water column and seafloor (Fig 4.1A; Fig 4.5; Box 4.4; Berge et al 2015a,b,c). Various Antarctic and Arctic macroalgae survive dark period of up to 18 months (Wiencke 1988, 1990a). We have often seen kelp down to 100-600 m depths, attached to wrecks and other structures at the seafloor indicating that they have survived in the darkness for more than one year using ROV surveys along Norwegian coast and Svalbard (Johnsen, Martinsen, Sørensen et al. unpublished data). Also, the attachment of macroalgae to sub-surface buoys at 30m depth indicates that macroalgae may grow very deep if they have a hard substrate to attach to (Box 4.5). To elucidate Polar Night eco-physiological responses in macroalgae we will illustrate this by two case studies - the arctic endemic species *Laminaria solidungula* and the boreal-arctic species *Saccharina latissima* (see comparison between species in section 4.5.3):

Case study I - *Laminaria solidungula*: The research by Dunton (1985) showed that *L. solidungula*'s new lamina started to develop in autumn initiated by shorter day lengths and that maximum growth rates occurred in the dark in late winter to early spring and declined under

well-lit conditions in summer and autumn (Alaskan Beaufort Sea). Peak growth period (1.4 mm day⁻¹) in *L. solidungula* was in late February to late April (Fig. 4.1; Fig 4.5A-B).

Some species of kelp do have perennial lamina that may be 1, 2 or 3 years old and with prominent annual differentiation and reflects that several years are needed to complete a life cycle (Wiencke et al. 2007; Belseth 2012; Shunatova et al. 2018; Scheschonk et al. 2019; Fig 4.5). In *L. solidungula* the 3 year old tissue in August-September typically show an empty sorus (fertile tissue where sporophytes are released), the two year old lamina shows a well-developed sorus (bright spade-like tissue) and the 1 year old part of the lamina showing brighter mid-part of lamina with developing and unmaturing sorus (Belseth 2012). The sorus is developed through winter, before growth of lamina begins, and spore release do not occur until the following spring (Hooper 1984). At latitudes of 80°N, this may be different. The oldest part of lamina is lost through abrasion and necrosis (Fig. 4.5), especially during autumn and winter time (own observations from 1996-2018; Carlsen et al. 2007; Belseth 2012). In contrast to the disc shaped hapter of *L. solidungula*, all other Svalbard kelp species obtain a hapter with several branches (fingers) grabbing the substrate.

The photobiological characteristics of *L. solidungula* specimens from Svalbard (Aug-Sep 2009 and 2010) did not fulfill all aspects of a “low light adapted algae”, characterized by high photosynthetic efficiency (α), low maximum photosynthetic rate (P_{max} , Belseth 2012) and low light saturation index (E_k , Sakshaug et al. 2009b). In the study by Belseth, the results from the meristem of *L. solidungula* obtained an E_k of 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (indicating high light acclimated tissue) whereas the 3-year old tissue of the same specimen obtained an E_k of 20 $\mu\text{mol m}^{-2} \text{s}^{-1}$. This study compared E_k of *L. solidungula* with 4 other kelp species from same locality and depth (3-5 m), i.e. *L. digitata*, *Saccorhiza dermatodea*, *Saccharina latissima* and *Alaria esculenta*, and indicated that *A. esculenta* was the most shade acclimated of the 5 species. *Alaria esculenta* is the kelp species we generally find in the deepest part of the sub littoral zone of Svalbard (own observations from 1996-2018). The E_k varies as a function of tissue age of a given specimen. Our observations indicate that *L. solidungula* is typically found beneath larger kelp species making a top canopy providing shade/low light conditions to be utilizing by the this low light adapted (shade) species relative to the larger kelp species (Fig 4.5A-B). But, in comparison to the four other dominant kelp species living in Svalbard waters, photosynthetic parameters of *L. solidungula* did not emphasize that this species is specially adapted to low light conditions, but we often found it in shallow and “shaded” areas in W, N, E Svalbard between and under the canopy of *L. digitata*/*S. nigripes* and *S. latissima*. Time-series of photosynthetic characteristics showed diurnal trends with highest quantum yield of photosynthetic charge separation of PSII during nighttime for all species investigated, Φ_{PSII} , close to the maximum limit of 0.75 for macroalgae, Belseth 2012; Aamot and Johnsen, unpublished; Scheschonk et al. 2019).

The meristem of juvenile individuals of *L. solidungula* from the Alaskan high Arctic exhibited E_k between 20 and 30 $\mu\text{mol m}^{-2} \text{s}^{-1}$ while the average E_k value of vegetative lamina in adult specimens was 38 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Dunton and Jodwalis 1988). This variation in E_k was also found in *L. solidungula* and *S. latissima* by Scheschonk et al. (2019).

Dunton (1990) showed that *Laminaria solidungula* in Alaskan Beaufort Sea at 70°N was exposed during August to September 1986 to total E_{sat} (daily period with $E_{PAR} > E_k$) periods of up to 148 h (indicating average daily E_{sat} of 3 h). Annual underwater E_{PAR} requirements have been estimated to be 45 $\text{mol m}^{-2} \text{yr}^{-1}$, the lowest ever documented for kelp populations globally. In comparison, the temperate *L. hyperborea*, received 71 $\text{mol m}^{-2} \text{yr}^{-1}$ (Lüning and Dring 1979).

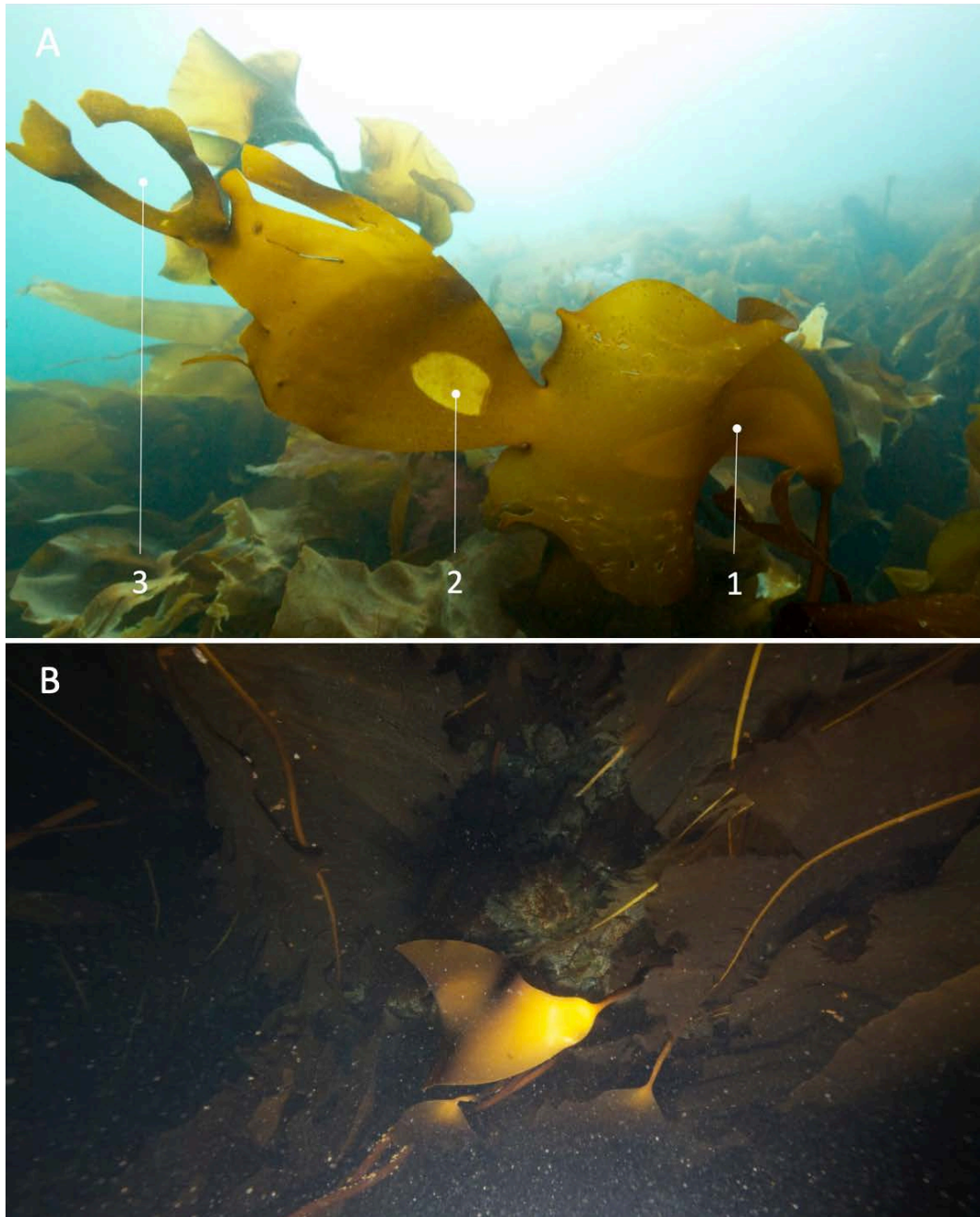


Fig 4.5. A) The endemic arctic kelp species *Laminaria solidungula* (Hinlopenstredet, Sep 2009). Tissue 1-3 denotes age (year) of lamina with different developmental stage of sorus (fertile tissue). 1 year old sorus (1) is clearly seen as a bright area from the basis of meristem (new growth), 2 year old sorus (2) is clearly seen as a bright spade shaped tissue. For the 3 year old tissue (3), the sporophytes has been released and providing hare-like ears (empty sorus). These characteristics, together with the small disc-shaped hapter (holdfast) are good criteria to identify and find this, sometimes “hard to find” species when SCUBA diving. B) Shows *L. solidungula* with new growth in meristem, induced by shorter photoperiods in September (Fig. 4.1A) is clearly seen as bright orange and newly formed tissue (centre of picture) surrounded by *A. esculenta* which have not started with significant growth (dark brown) in late autumn. Picture from 20 m depth at Ryke Yse Island, E-Svalbard Sep 2011. The bright yellow colour is

due to high fucoxanthin: Chl a ratio, cf. Johnsen et al. (2016) (see Table 4.1). Photos: Geir Johnsen.

Case study II - *Saccharina latissima*: In comparison to the endemic Arctic species *L. solidungula*, the boreal-Arctic species *S. latissima* appears to delay nearly all of its annual growth (maximum growth of 4.7 mm day⁻¹) to a brief period in late April to July in well illuminated water column starting at sea ice break-up (Dunton 1985; Fig. 4.1). In a current study (Aamot and Johnsen, unpublished), winter values of E_k did not vary significantly between individuals at meristem, mid or top part of lamina in *S. latissima* from W-Spitsbergen and Trondheimsfjorden (63°N, mid-Norway). This was also found by Scheschonk et al. (2019). In the study by Aamot and Johnsen, *S. latissima* data was collected from specimens from Polar Night in January 2013 and 2014 in W-Spitsbergen (78-79°N) and data from specimens during Dec-Feb 2014-2015 from Trondheimsfjord (mid-Norway) with specimens exposed to ambient light or in darkness, simulating Polar Night. However, in the Arctic specimen of *S. latissima*, top tissue (oldest part) values of E_k were found to be significantly lower than meristem values, in contrast to specimens from the Trondheimsfjord. For all specimens of *S. latissima* (both Svalbard and Trondheimsfjord) non photochemical quenching (NPQ) increased significantly with increasing irradiance during rapid light curve (RLC) experiments. In the “Arctic Polar Night” individuals from Svalbard, the rise in NPQ with increased irradiance (E_{PAR} , 0 to ~ 900 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) also varied between lamina sections and with significantly higher NPQ in the meristem compared to mid and top (older tissue) sections at all $E_{PAR} > 350 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. In the meristem tissue, there were no significant differences between Arctic and Trondheimsfjorden specimens of *S. latissima* (in dark or in light) in maximum quantum yield of PSII fluorescence ($\Phi_{PSII\text{max}}$) at any time point during the recovery studies. After 25 minutes in dark after RLC experiments, the $\Phi_{PSII\text{max}}$ stabilized at 95-100 % of initial dark value (before RLC) for all specimens. Both Chl c and fucoxanthin concentration per wet weight was significantly lower in the meristem of “Trondheimsfjorden dark” compared to “Arctic Polar Night” individuals, indicating that the latter is more shade adapted. In contrast to *L. solidungula*, *S. latissima* is found along coastal regions in northern Europe such as along North Sea coast (Helgoland, Germany), along the Norwegian coast, to the northernmost tip in Svalbard, at Rossøya (Fig 4.2). This indicates that *S. latissima* is surviving over a large range of different light regimes, and this can be considered a photobiological “generalist” compared to *L. solidungula* which is more a “specialist” surviving the extreme light regime of the high Arctic only.

4.5.3 Survival in the Polar Night darkness – *L. solidungula* vs *S. latissima*

In this section we discuss the differences in eco-physiology between *L. solidungula* and *S. latissima* during the Polar Night (Fig 4.1A, Fig 4.5A-B). The energy required to survive and start lamina formation during the Polar Night is done by mobilization of stored carbon reserves, accumulated during summer, when inorganic nitrogen is high (winter values, Wiencke et al. 2007; Schoschenk et al. 2019). In *L. solidungula* the utilization of these reserves occurs during Polar Night and also, sometimes, under thick sea-ice (note that ice cover nowadays is greatly reduced), completing >90% of its annual linear growth, inducing a carbon deficit before photosynthetic production begins in early summer (Dunton and Schell 1986). A young (8 cm total length) specimen of *L. solidungula*, sampled in January 2010 in Kongsfjorden, not been exposed to actinic light from the sun in its lifetime, did respond to actinic E_{PAR} (using Diving PAM *in situ* illuminated with artificial light) due to functional photosynthetic pigments in the chloroplasts and the ability to provide photosynthetic electron transfer (Belseth 2012). The specimen, however, responded quite slowly to light exposure by means of photosynthesis

versus irradiance curve with an E_k of $81 \mu\text{mol m}^{-2} \text{s}^{-1}$, implying that it needed high amounts of E_{PAR} to saturate photosynthesis. This may be due to that not all light harvesting complexes were efficient in light energy transfer and that many of the D1 proteins in photosystem II were not active or partly degraded. Regarding pigments and photosynthetic performance, this specimen of *L. solidungula* had 1.8 times more fucoxanthin than Chl a (w:w ratio) in contrast 0.8-0.9 for specimens sampled in Aug-Sep. This have also clearly been seen *in situ* as bright orange meristem in Polar Night and individual of fucoxanthin rich tissue relative to the darker and older tissue which appears dark brown by eye caused by a higher fraction of Chl a and Chl c_{1+2} (Belseth and Johnsen unpublished data, Fig 4.5B). This is also a general feature for *L. digitata* and *S. latissima* at winter time along the Norwegian coast, with bright orange parts of lamina indicating new laminar tissue relative to darker brown and older lamina detected by ROV-based underwater hyperspectral imaging (UHI) (Johnsen et al. 2016; see Chapter 9 and 10). This in contrast to findings by Schoschenk et al. (2019) that found little differences in pigments ratios and concentration in lamina of *L. solidungula* and *S. latissima*.

Important environmental cues inducing sorus formation (Lüning 1990) and new lamina formation (growth) in several species of kelp (Lüning 1990) are **the onset of short day lengths** in autumn together with **lower temperatures and normally, low levels of nitrate** (N source taken up during summer period by both phytoplankton and macroalgae (Lüning and tom Dieck 1989). Of all these environmental cues, experimental studies demonstrated that **day length was most important in the setting of internal clocks** in species that possess circannual rhythms which control the periodicity in linear growth (Fig. 4.1; Fig 4.5; Lüning 1990; Chapter 3 and 8).

As temperatures and nutrient levels show only a small variation over the year in Antarctic waters, seasonality of Antarctic macroalgae depends mainly on variable light conditions and, especially, daylength. Data from Arctic species are so far based on field studies only (Wiencke et al. 2007; Scheschonk et al. 2019; unpublished data).

Mannitol, is probably the major substrate for respiration during the period of active kelp growth during the arctic Polar Night. This is reflected by its low mannitol concentration in tissues during winter growth period. In late summer, the mannitol content increases significantly in the basal (meristem) and middle region. In the distal region it may serve as substrate for light independent carbon fixation or stored as laminaran (storage glucan) which attains its highest content in the distal thallus part (Gomez and Wiencke 1998). Scheschonk et al. (2019) concluded that laminaran content was reduced by 95 and 90 % during polar Night in *S. latissima* and *L. solidungula*, respectively, fueling metabolic functions. They concluded that differences in laminaran content between the two species and across different regions of lamina indicated species specific adaptive mechanisms between boreal-temperate and Arctic-endemic kelp. *Laminaria solidungula* is one of many kelp species that have evolved physiological responses, such as storing nutrients-rich compounds when nutrient supply is high during winter darkness, to avoid nutrient competition with other phototrophic organisms (Wiencke et al. 2007; Bartsch et al. 2008).

Nitrogen to carbon ratios (N:C, at:at) are generally high (indicating ample NO_3 in water) in spring and low in summer (N-limitation) for kelp species. In Svalbard, *L. solidungula* N:C ratios were highest in May (0.08) and lowest in August (0.03-0.05). For the 8 cm specimen sampled during Polar Night in January 2010, the N:C ratio was 0.06 (Belseth 2012). In August, *L. digitata*, *S. latissima*, *A. esculenta* and *Saccorhiza dermatodea* obtained N:C ratios ranging from 0.04-0.06 (Belseth 2012). In mid Norway (63°N), the monthly average N:C ratio were lowest from June-September for *S. latissima* (≈ 0.03 for both old and meristem tissue) and around 0.08 from October – May (highest values in the meristem with N:C ratios around 0.1-1.2 in Dec-Feb (Hilstad 2005).

4.6 Conclusive remarks

We now know that the Polar Night is not a dark and idle season. In contrast, the Polar Night is critical in shaping the biological activity in the Arctic spring providing time for growth, development, resting and alternative life strategies. Microalgae have unique adaptations including life cycles and ecophysiology that allows them to rapidly grow once light comes back in spring, while some macroalgae can utilize the Polar Night for growth.

For microalgae, resting stages and mixotrophy appear to be adaptive traits to survive the winter season. One could argue that at high latitudes, an alternative food web based on mixotrophy may dominate the pelagic lower food web during much of the year, causing a unique functioning of the microbial network. Alternatively, many Arctic sea ice and pelagic microalgae and macroalgae have evolved astonishing capabilities to survive months of complete darkness based on reduced metabolism and/or the use of energy reserves in form of carbohydrates or lipids. Additionally, the complex life cycles of microalgae do include specialized cell types build to last long periods without being attacked by bacteria or animals. These cysts can overwinter on the sea floor and re-germinate once conditions are favorable in spring.

Still, our knowledge regarding the Polar Night ecosystem is limited and new discoveries might challenge the current views. To improve our ability to predict future changes in the key processes during the crucial phase of winter–spring transition, we need to increase our knowledge about overwintering strategies of key species, and the origin of the “seed populations” of phytoplankton and ice algal blooms. This is important for understanding winter biodiversity and food web interactions and study so far neglected habitats like benthic microalgae in their seasonal changing contribution to the Arctic marine food web.

Some macroalgal species may act as “season anticipators“ and utilize the winter darkness or initial spring period as major growth seasons. We have used two kelp species as examples of two different growth strategies, i.e. an endemic Arctic kelp species actively growing during the Polar Night with laminar growth by mobilization of stored carbon reserves, accumulated during summer, when inorganic nitrogen is high. In contrast, a boreal-arctic kelp species obtaining maximum laminar growth during a brief period in late April to July in well illuminated water column starting at sea ice break-up. Reduced sea-ice cover and thickness will change this “normal scenario”.

In the Arctic, kelp is predicted to expand in distribution, especially vertically due to reduced ice-scouring. The kelp forests are currently extending the distribution starting at 3 m depth towards surface due to absence of sea-ice. Kelp forests contribute significantly to overall marine biodiversity also including fish species from greater depths coming to surface waters during the Polar Night, possibly to reproduce and find prey. We lack knowledge on the overall bio-diversity, ecology and physiology of annual and perennial species of macroalgae. Associated fauna and the kelp forest play ecologically important roles as habitat, shelter and feeding areas for a large range of invertebrates, fish, mammals and sea birds. Both biotic and abiotic factors, including habitat stability and proximity to source populations, contribute to these spatial and temporal patterns in algal and faunal abundance and diversity in the kelp forest.

To provide a knowledge-based management of polar marine systems including marine micro- and macroalgae in general and e.g. kelp forests we need to identify, map and monitor these habitats using new enabling technology using autonomous instrument carrying platforms and sensors, elucidated in Chapter 9 and 10. In addition, we need to combine information from several disciplines comprising biology (molecular biology, ecologists and physiologists), chemistry (eg. elemental composition in algae), oceanography, geography and technology to combine all the information to enhance information and knowledge for a better understanding and management to provide clever and fast decisions.

Abiotic & biotic variables versus 0-30 m depth:

Ice scouring (duration)

Competition for
substrate & space

Sedimentation

Nutrients

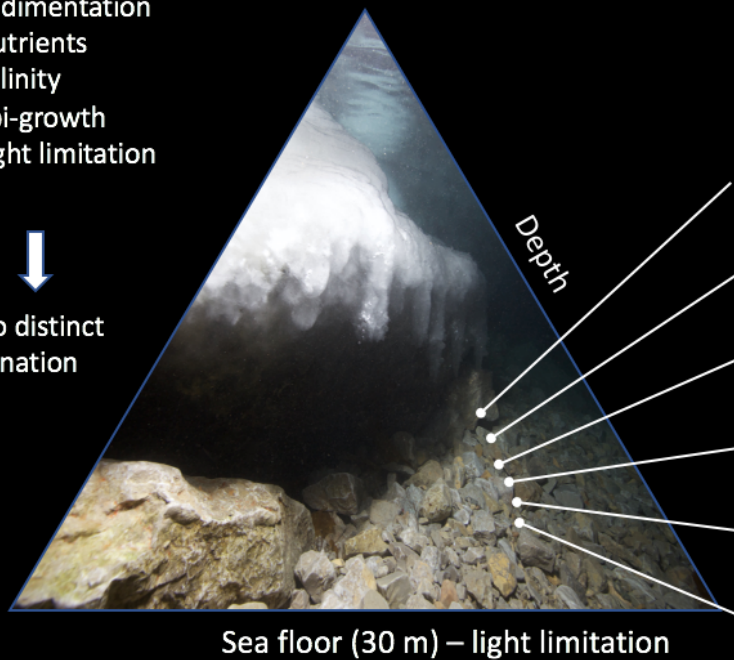
Salinity

Epi-growth

Light limitation

Surface - ice scouring

↓
No distinct
zonation



Sea floor (30 m) – light limitation

Major perennial species:

Fucus distichus



Laminaria digitata



Saccharina nigripes



Saccharina latissima



Palmaria palmata

Saccorhiza dermatodea



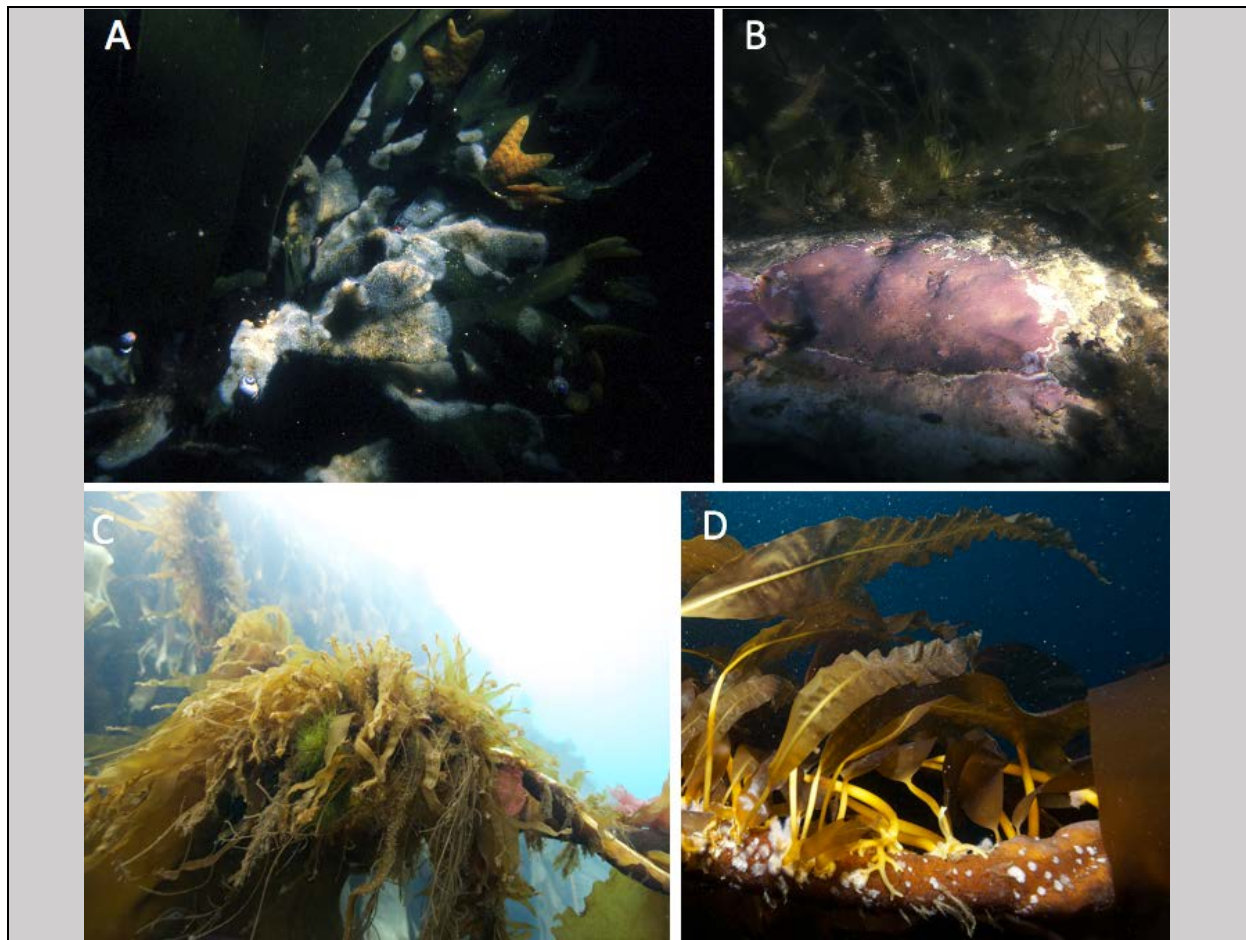
Laminaria solidungula

Alaria esculenta

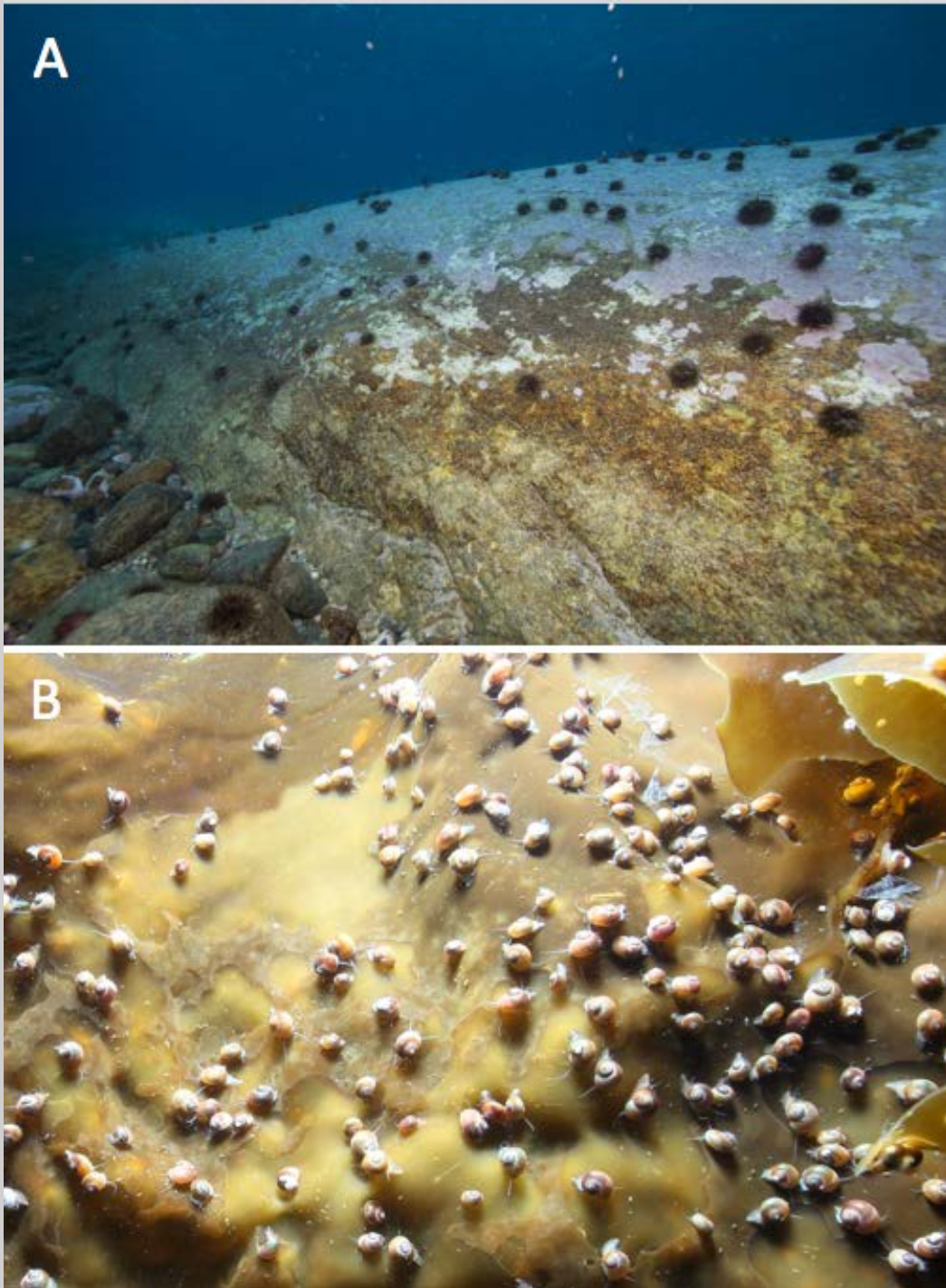


Coralline red algae

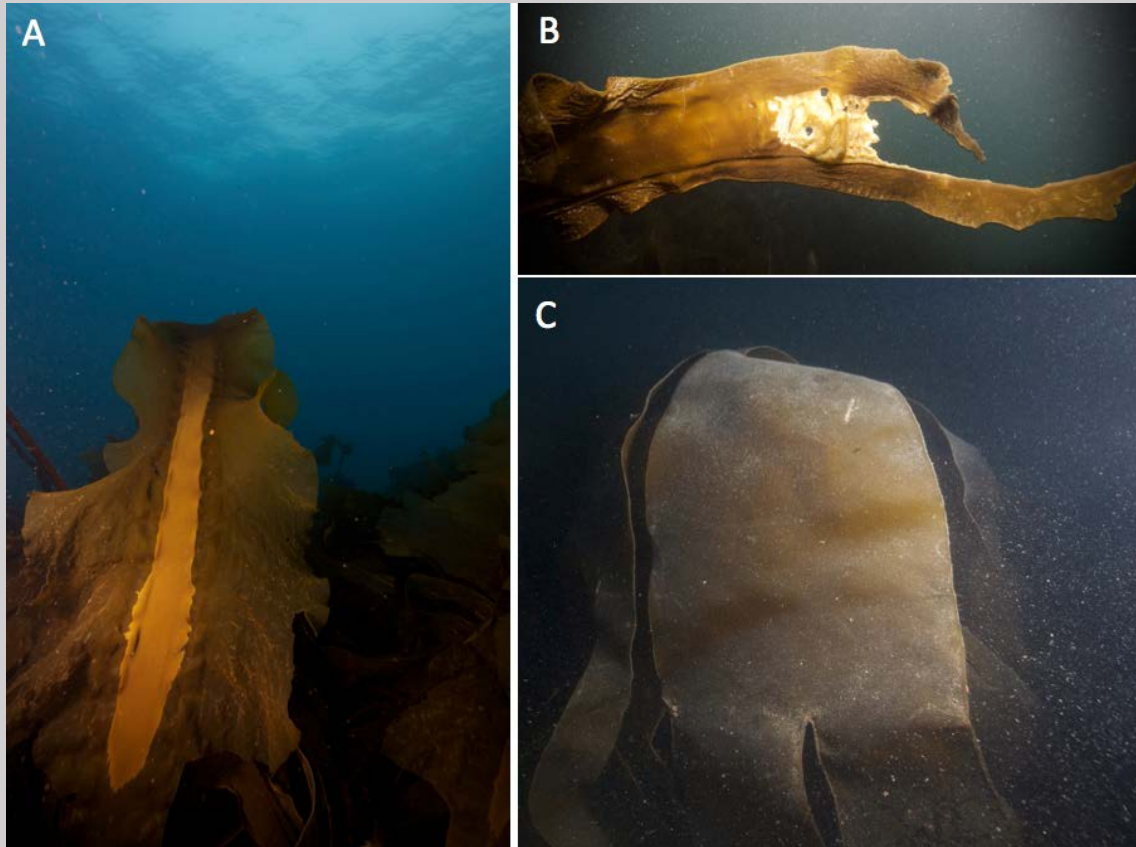
Box 4.1. Absence of distinct macroalgal zonation due to abiotic and biotic variables. The major variables affecting macroalgal biodiversity in the eulittoral zone (0-3m) is ice-scouring: Heavy ice-scouring may leave the upper 4 m barren and only with annual species growing as “bio-film” in summer months. Perennial species are found in cracks and in between rocks. There is a zone devoid of ice-scouring and providing enough light for photosynthesis (4-30 m) that is optimal for algal growth and thus a high competition for space and substrate for brown, red and green macroalgae. Due to lack of space, a given kelp species may be overgrown (epigrowth) of several other macroalgal species (ref to other fig?). During period of fresh water run-off (May-Oct) upper 15 m are highly affected by sedimentation and low salinities, especially in Svalbard fjords. During winter time, high nutrient concentrations (without competition of phytoplankton) allows tissue growth at full salinity. Water transparency very good from October to May due to no fresh water run-off. Epigrowth is accumulating from May-Nov. The major perennial species and approximate vertical distribution is indicated. Image shows an ice foot (Kongsfjorden, Jan) from 0-1.5 depth and zone beneath is barren due to ice-scouring and sea-ice following the diurnal tidal cycle (tidal amplitude approximately ± 1.3 m in this area).



Box 4.2. Epigrowth on macroalgae. A. The wrack *Fucus distichus* with epigrowth of bryozoans and *Margarites* sp. Kongsfjorden, 1 m depth, September. B. Coralline red algae produces substances for biological “warefare” to avoid being overgrown (Kongsfjorden, July). The dead part of coralline red algae (white part) is slowly started to be overgrown by macroalgae. C. One large specimen of *Saccharina latissima* (Hinlopen strait, August) may be up to 5 m in length since lamina may be old (at least 3 years old) and with a stipes that may be older than 8 years. Such old and well-developed stipes makes an important substrate for many species of green, red and brown macroalgae. D. Juvenile specimens of *Alaria esculenta* growing on an older specimen. Photos: Geir Johnsen.



Box 4.3. Grazing of macroalgae. A. The urchin *Strongylocentrotus droebachiensis* grazes both on kelp and coralline algae. Rijpfjorden, Nordaustlandet, Svalbard (Sep). B. During autumn and winter, protein rich sorus regions of kelp, such as *Saccharina latissima* pictured here, may be visited by a high number of *Margarites* spp. The snails are mainly grazing on the protein rich sorus area of the lamina (Jan, Kongsfjorden). Photos: Geir Johnsen.



Box 4.4. Fertile tissue (sorus) of kelp (all images taken autumn, W and N Spitsbergen). A. *Saccharina latissima* with sorus in central parts of lamina. B. *Saccharina latissima* with degraded sorus with released sporophytes. C. *Saccharina nigripes/Laminaria digitata* -species complex with sorus covering most of lamina (C). Photos: G. Johnsen.



Box 4.5. Growing in the dark. A. A buoy taken up from 30 m depth after being 1 year in the water column, Kongsfjorden, August 2010. This indicates that macroalgae may grow quite fast in coastal waters influenced by river run-off at 30 m depth if a hard substrate (buoy) is provided. B. The epigrowth on buoy in picture A was dominated by the kelp *Alaria esculenta* were the largest specimens grew to 1 m length in one year. Also, two specimens of *dermatodea* was attached to the buoy together with the bryozoan *Alcyonidium gelatinosum*, the bivalve *Hiatella arctica* and the cirriped *Semibalanus balanoides*. C. Green alga in January, possibly *Monostroma* sp. (Kongsfjorden). D. Dense concentration of stipes from *S. latissima* dominated with bryozoan epigrowth (January, Kongsfjorden). This an important habitat for hydroids, bryozoans, polychaetes, echinoderms, bivalves, snails (*Buccinum undatum*, *Margarites* sp. and nudibranchs), crustaceans (shrimps, mysids and *Hyas araneus*) and fish (polar and atlantic cod). E. The red algae, *Palmaria palmata*, in January with new and apparently fresh tissue (Kongsfjorden). Photos: Geir Johnsen.

References

- Aamot I, Pokrzywinski K, Johnsen G, Berge J, Sørensen A (2014) Light climate and status of the photosynthetic machinery in macroalgae in the polar night. Ocean Optics, Portland, Maine, USA, Oct 30. Ext. abstr 2050. Pp. 15
- Aguirre J, Riding R, Braga JC (2000) Diversity of coralline red algae: Origination and extinction patterns from the early Cretaceous to the Pleistocene". *Paleobiol* 26: 651–667. doi:10.1666/0094-8373(2000)026<0651:DOCRAO>2.0.CO;2
- Assmy P, Fernández-Méndez M, Duarte P, Meyer A, Randelhoff A, Mundy CJ, Olsen LM, Kauko HM, Bailey A, Chierici M, Cohen L, Doulgeris AP, Ehn JK, Fransson A, Gerland S, Hop H, Hudson SR, Hughes N, Itkin P, Johnsen G, King JA, Koch BP, Koenig Z, Kwasniewski S, Laney SR, Nicolaus M, Pavlov AK, Polashenski CM, Provost C, Rösel A, Sandbu M, Spreen G, Smedsrud LH, Sundfjord A, Taskjelle T, Tatarek A, Wiktor J, Wagner PW, Wold A, Steen H, Granskog MA (2017) Leads in Arctic pack ice enable early phytoplankton blooms below snow-covered sea ice. *Sci Rep* 7:40850 DOI:10.1038/srep40850
- Bartsch I, Wiencke C, Bischof K, Buchholz CM and others (2008) The genus *Laminaria* sensu lato: recent insights and developments. *Eur J Phycol* 43:1–86
- Bartsch I, Paar M, Fredriksen S, Schwanitz M, Daniel C, Hop H, Wiencke C (2016) Changes in kelp forest biomass and depth distribution in Kongsfjorden, Svalbard, between 1996–1998 and 2012–2014 reflect Arctic warming. *Polar Biol* 39:2021–2036
- Berge J, Cottier F, Last K, Varpe Ø, Leu E, Søreide J, Eiane K, Falk-Petersen S, Willis K, Nygård H, Voegedes D, Griffiths C, Johnsen G, Lorenzen D, Brierley AS (2009) Diel vertical migration of Arctic zooplankton during the polar night. *Biol Lett* Doi:10.1098/rsbl.2008.0484
- Berge J, Johnsen G, Sørensen, Nilssen I (2015a) Enabling technology for Arctic research. *Pan European Networks: Science and Technology Magazine* 15:199-201
- Berge J, Daase M, Renaud PE, Ambrose WG, Darnis G, Last KS, Leu E et al. (2015b) Unexpected levels of biological activity during the polar night offer new perspectives on a warming Arctic. *Curr Biol* 25:2555–61
- Berge J, Renaud PE, Darnis G, Cottier F, Last K, Gabrielsen TM, Johnsen G et al. (2015c) In the dark: a review of ecosystem processes during the Arctic polar night. *Prog Oceanogr* 139:258–71
- Błachowiak-Samołyk K, Wiktor JM, Hegseth EN, Wold A, Falk-Petersen S, Kubiszyn AM (2015) Winter tales: the dark side of planktonic life. *Polar Biol* 38:23–36
- Bluhm BA, Gradinger R (2008) Regional variability in food availability for Arctic marine mammals. *Ecol Appl* 18:77-96
- Bosence DWJ (1980) Sedimentary facies, production rates and facies models for recent coralline algal gravels. *Geol J* 15:91–111
- Brown T, Hegseth EN, Belt S (2015) A biomarker-based investigation of the mid-winter ecosystem in Rijpfjorden, Svalbard. *Polar Biol* 38:37–50
- Bunt JS, Lee CC (1972) Data on the composition and dark survival of four sea-ice microalgae. *Limnol Oceanogr* 17. doi.org/10.4319/lo.1972.17.3.0458
- Burdett HL, Hennige SJ, Francis FTY, Kamenos NA (2012) The photosynthetic characteristics of red coralline algae, determined using pulse amplitude modulation (PAM) fluorometry. *Bot Mar* 55:499–509
- Cahoon LB (1999) The role of benthic microalgae in neritic ecosystems. *Oceanogr Mar Biol Ann Rev* 37:47-86

- Carlsen BP, Johnsen G, Berge J, Kuklinski P (2007) Biodiversity pattern of macro-epifauna on different parts of *Laminaria digitata* and *Saccharina latissima* collected during spring and summer 2004 in Kongsfjorden, Svalbard. *Polar Biol* 30:939-943
- Demmig-Adams B, Adams III WW (1992) Photoprotection and other responses of plants to high light stress. *Annu Rev Plant Physiol Plant Mol Biol* 43:599-626
- Druzhkov N, Druzhkova E, Kuznetsov L (2001) The sea-ice algal community of seasonal pack ice in the southwestern Kara Sea in late winter *Polar Biol* 24:70-72
doi.org/10.1007/s003000000185
- Druzhkova E, Oleinik A, Makarevich P (2017) Live autochthonous benthic diatoms on the lower depths of Arctic continental shelf. Preliminary results. *Oceanologia* 60:97-100
doi.org/10.1016/j.oceano.2017.07.001
- Dunton KH (1985) Growth of dark-exposed *Laminaria saccharina* (L.) Lamour. and *Laminaria solidungula* J. Ag. (Laminariales: Phaeophyta) in the Alaskan Beaufort Sea. *J Exp Mar Biol Ecol* 94:181-189
- Dunton KH (1990) Growth and production in *Laminaria solidungula*: relation to continuous underwater light levels in the Alaskan high Arctic. *Mar Biol* 106:297-304.
- Dunton KH, Jodwalis CM (1988) Photosynthetic performance of *Laminaria solidungula* measured in situ in the Alaskan High Arctic. *Mar Biol* 98:277-285
- Dunton KH, Schell DM (1986) Seasonal carbon budget and growth of *Laminaria solidungula* in the Alaskan High Arctic. *Mar Ecol Prog Ser* 31:57-66
- Falkowski PG, Raven JA (1997) Aquatic photosynthesis. Blackwell Science, Oxford
- Forbord S (2004) Annual variation in pigmentation in marine red, brown and green macroalgae. Cand Scient thesis, NTNU Trondheim. 105 pp
- Fredriksen S, Bartsch I, Wiencke C (2014) New additions to the benthic marine flora of Kongsfjorden, western Svalbard, and comparison between 1996/1998 and 2012/2013. *Bot Mar* 57. <https://doi.org/10.1515/bot-2013-0119>
- Freiwald A, Henrich R (1994) Reefal coralline algal build-ups within the Arctic circle: morphology and sedimentary dynamics under extreme environmental seasonality. *Sedimentology* 41:963-84
- Glud RN, Woelfel J, Karsten U, Kühl M, Rysgaard S (2009) Benthic microalgal production in the Arctic: applied methods and status of the current database. *Bot Mar* 52:559-571. DOI 10.1515/BOT.2009.074
- Glud RN, Kühl M, Wenzhoefer F, Rysgaard S (2002) Benthic diatoms of a high Arctic fjord (Young Sound, NE Green-land): importance for ecosystem primary production. *Mar Ecol Progr Ser* 238:15-29
- Gomez I, Weykam G, Klöser H, Wiencke C (1997) Photosynthetic light requirements, daily carbon balance and zonation of sublittoral macroalgae from King George Island (Antarctica). *Mar Ecol Progr Ser* 148:281-293
- Goto N, Mitamura O, Terai H (2001) Biodegradation of photosynthetically produced extracellular organic carbon from intertidal benthic algae. *J Exp Mar Biol Ecol* 257:73-86
doi.org/10.1016/S0022-0981(00)00329-4
- Gradinger R (2009) Sea-ice algae: Major contributors to primary production and algal biomass in the Chukchi and Beaufort Seas during May/June 2002. *Deep Sea Res II* 56:1201-1212
DOI: 10.1016/j.dsr2.2008.10.016
- Gradinger R, Ikävalko J (1998) Organism incorporation into newly forming Arctic sea ice in the Greenland Sea. *J Plankton Res* 20:871-886. doi.org/10.1093/plankt/20.5.871
- Grzyski J, Johnsen G, Sakshaug E (1997) The significance of intracellular self-shading on the bio-optical properties of brown, red and green macroalgal species. *J Phycol* 33:408-414
- Hanelt D (1998) Capability of dynamic photoinhibition in Arctic macroalgae is related to their depth distribution. *Mar Biol* 131:361-369

- Hilstad K (2005) In situ tidsseriemålinger av lyshøstingsegenskaper og cellekjemi hos marine makroalgaer i Trondheimsfjorden. Cand scient thesis, NTNU, Trondheim, 113 pp
- Hooper RG (1984) Functional adaptations to the polar environment by the arctic kelp, *Laminaria solidungula*. *Br Phycol J* 19:194
- Hop H, Wiencke C, Vögele B, Kovaltchouk NA (2012) Species composition, zonation, and biomass of marine benthic macroalgae in Kongsfjorden, Svalbard. *Bot Mar* 55:399–414
- Hop H, Kovaltchouk NA, Wiencke C (2016) Distribution of macroalgae in Kongsfjorden, Svalbard. *Polar Biol* 39:2037–2061. DOI 10.1007/s00300-016-2048-1
- Horner RA, Alexander V (1972) Algal populations in arctic sea ice: an investigation of heterotrophy. *Limnol Oceanogr* 17:454–458
- Horner R, Schrader GC (1982) Relative contribution of ice algae, phytoplankton, and benthic microalgae to primary production in nearshore regions of the Beaufort Sea. *Arctic* 35:485–503
- Hsiao SIC (1992) Dynamics of ice algae and phytoplankton in Frobisher Bay. *Polar Biol* 12: 645–651 doi.org/10.1007/BF00236987
- Hurd CL, Harrison PJ, Bischof K, Lobban CS (2014) Seaweed ecology and physiology. Cambridge University Press, Oxford, 2nd edition. 551 pp
- Irving AD, Connell SD, Elsdon TS (2004) Effects of kelp canopies on bleaching and photosynthetic activity of encrusting coralline algae. *J Exp Mar Biol Ecol* 310:1–12
- Isaksen K, Nordli Ø, Førland EJ, Łupikasza E, Eastwood S, Niedźwiedź T (2016) Recent warming on Spitsbergen – Influence of atmospheric circulation and sea ice cover *J Geophys Res: Atmospheres* 121:11913–11931. doi:10.1002/ 2016JD025606
- Iversen KR, Seuthe L (2011) Seasonal microbial processes in a high-latitude fjord (Kongsfjorden, Svalbard): I. Heterotrophic bacteria, picoplankton and nanoflagellates. *Polar Biol* 34:731–749. DOI 10.1007/s00300-010-0929-2
- Jeffrey SW, Wright SW, Zapata M (2011) Microalgal classes and their signature pigments, pp. 3–77. In: *Phytoplankton Pigments: Characterization, Chemotaxonomy and Applications in Oceanography*, Roy S, Llewellyn CA, Egeland ES, Johnsen G (eds) Cambridge University Press ISBN 9780511732263
- Johnsen G, Eikrem W, Dalløkken R, Legrand C, Aure J, Skjoldal HR (1999) Eco-physiology, bio-optics and toxicity of the ichthyotoxic prymnesiophyte *Chrysochromulina leadbeateri*. *J Phycol* 35:1465–76
- Johnsen G, Sakshaug E (2007) Bio-optical characteristics of PSII and PSI in 33 species (13 pigment groups) of marine phytoplankton, and the relevance for PAM and FRR fluorometry. *J Phycol* 43:1236–1251
- Johnsen G, Volent Z, Sakshaug E, Sigernes F, Pettersson LH (2009) Remote sensing in the Barents Sea. Pp 139–166. In Sakshaug E, Johnsen G, Kovacs K (eds) *Ecosystem Barents Sea*. Tapir Academic Press, Trondheim ISBN 978-82-519-2461-0
- Johnsen G, Bricaud A, Nelson N, Prézelin BB, Bidigare RR (2011) *In vivo* bio-optical properties of phytoplankton pigments. In: *Phytoplankton pigments: Updates on Characterization, Chemotaxonomy and Applications in Oceanography*. Roy S, Llewellyn C, Egeland E, Johnsen G [Eds] Cambridge University Press Chapter 13:496–537 Cambridge,UK. ISBN: 978110700066-7
- Johnsen G, Ludvigsen M, Sørensen A, Aas LM (2016) The use of underwater hyperspectral imaging deployed on remotely operated vehicle – methods and applications. *IFAC papersOnLine* 49:476–481
- Johnsen G, Norli M, Moline M, Robbins I, Quillfeldt CV, Sørensen K, Cottier F, Berge J (2018) The advective origin of an under-ice spring bloom in the Arctic Ocean using multiple observational platforms. *Polar Biol* 41:1197–1216. DOI: 10.1007/s00300-018-2278-5

- Jørgensbye HIØ, Halfar J (2017) Overview of coralline red algal crusts and rhodolith beds (Corallinales, Rhodophyta) and their possible ecological importance in Greenland. *Polar Biol.* 40:517-531. DOI 10.1007/s00300-016-1975-1
- Kauko HM, Taskjelle T, Pavlov AK, Mundy CJ, Assmy P, Duarte P, Fernández Méndez M, Olsen LM, Hudson SR, Johnsen G, Granskog MA (2017) Windows in Arctic sea ice: light transmission and the role of ice algae in a refrozen lead. *J Geophys Res.* 122:1486-1505. DOI: 10.1002/2016JG003626
- Kauko HM, Olsen LM, Duarte P, Peecken I, Granskog M, Johnsen G, Fenandez-Méndez M, Pavlov A, Mundy CJ, Assmy P (2018). Algal colonization of young Arctic sea ice in spring. *Frontiers in Marine Science, Marine Syst Ecol.* doi: 10.3389/fmars.2018.00199
- Olsen, L. M. et al (2017), The seeding of ice algal blooms in Arctic pack ice: The multiyear ice seed repository hypothesis, *J Geophys Res Biogeosci* 122:1529–1548, doi:10.1002/2016JG003668.
- Kleiven W, Johnsen G, Ardelan MV (2019) Sea surface micro layer and elemental composition in Phaeo-, Chloro- and Rhodophytes in winter and spring. *J Phycol* DOI: 10.1111/jpy.12851
- Kruss A, Tegowski J, Tatarek A, Wiktor J, Blondel P (2017) Spatial distribution of macroalgae along the shores of Kongsfjorden (West Spitsbergen) using acoustic imaging. *Polish Pol Res.* 38:205-229. doi: 10.1515/popore-2017-0009
- Kvernvik AC, Hoppe CJM, Lawrens E, Prazil, O, Greenacre M, Wiktor JM, Leu E (2018) Fast reactivation of photosynthesis in arctic phytoplankton during the polar night. *J. Phycol.* DOI: 10.1111/jpy.12750
- Last KM, Hobbs L, Berge J, Brierley AS, Cottier F (2016) Moonlight drives ocean-scale mass vertical migration of zooplankton during the Arctic winter. *Curr Biol* 26:244-251
- Ludvigsen M, Berge J, Geoffroy M, Cohen JH, De La Torre PR, Nornes SM, Singh H, Sørensen AJ, Daase M, Johnsen G (2018) Use of an Autonomous Surface Vehicle reveal new zooplankton behavioral patterns and susceptibility to light pollution during the polar night. *Sci Adv* 4 (1), eaap9887. DOI: 10.1126/sciadv.aap9887
- Leu E, Søreide JE, Hessen DO, Falk-Petersen S, Berge J (2011) Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelf seas: Timing, quantity, and quality". *Progr Oceanogr Arctic Marine Ecosystems in an Era of Rapid Climate Change.* 90 (1–4): 18–32. doi:10.1016/j.pocean.2011.02.004
- Leu E, Mundy CJ, Assmy P, Campbell K, Gabrielsen TM, Gosselin M, Juul-Pedersen T, Gradinger R (2015) Arctic spring awakening – Steering principles behind the phenology of vernal ice algal blooms. *Progr Oceanogr* 139:151-170
- Lund L, Lydon A, Johnsen G, Gabrielsen TM, Moline MA, Bakken T (2019) The kelp *Saccharina nigripes* is abundant in Svalbard, in prep
- Lüning K, Dring M (1979) Continuous underwater light measurements near Helgoland (North Sea) and its significance for characteristic light limits in the sublittoral region. *Helgol Mar Res* 32:403–424
- Lüning K (1990) *Seaweeds: their environment, biogeography, and ecophysiology*, 2nd edn. John Wiley & Sons, New York
- Lüning K, tom Dieck I (1989) Environmental triggers in algal seasonality. *Bot Mar* 32:389–397
- Manes SS, Gradinger R (2009) Small scale vertical gradients of Arctic ice algal photophysiological properties. *Photosynth Res* 102:53-66
- Marquardt M et al. (2016) Strong Seasonality of Marine Microbial Eukaryotes in a High-Arctic Fjord (Isfjorden, in West Spitsbergen, Norway). *Appl Envir Microbiol* 82:1868-1880
- Martone PT, Alyono M, Stites S (2010) Bleaching of an intertidal coralline alga: untangling the effects of light, temperature and desiccation. *Mar Ecol Prog Ser* 416:57–67

- McCoy SJ, Kamenos NA (2015) Coralline algae (Rhodophyta) in a changing world: Integrating ecological, physiological, and geochemical responses to global change. *J Phycol* 51:6-24. DOI: 10.1111/jpy.12262
- McKie-Krisberg ZM, Sanders RW (2014) Phagotrophy by the picoeukaryotic green alga *Micromonas*: implications for Arctic Oceans. *ISME* 8:1953-1961
- McMinn A, Martin A (2013) Dark survival in a warming world. *Proc R Soc B* 280:20122909. <http://dx.doi.org/10.1098/rspb.2012.2909>
- Mock T, Gradinger R (1999) Determination of Arctic ice algal production with a new in situ incubation technique. *Mar Ecol Prog Ser* 177:15-26
- Niemi A, Michel C, Hille K, Poulin M (2011) Protist assemblages in winter sea ice: setting the stage for the spring ice algal bloom. *Polar Biol* 34:1803-1817
- Nymark M, Valle KC, Brembu T, Hancke K, Winge P, Andresen K, Johnsen G, Bones AM (2009) An integrated analysis of molecular acclimation to high light in the marine diatom *Phaeodactylum tricorutum*. *PloS ONE* 11:e7743. doi:10.1371/journal.pone.0007743
- Nymark M, Valle KC, Winge P, Hancke K, Andresen K, Johnsen G, Bones A, Brembu T (2013) Molecular and photosynthetic responses to prolonged darkness and subsequent acclimation to re-illumination in the diatom *Phaeodactylum tricorutum*. *PlosOne*, 8 (3) e58722
- Olsen LM, Öztürk M, Sakshaug E, Johnsen G (2006) Photosynthesis-induced phosphate precipitation in seawater: ecological implications for phytoplankton. *Mar Ecol Prog Ser* 319:103-110
- Olsen LM, Laney SR, Duarte P et al. (2017) The seeding of ice algal blooms in Arctic pack ice: The multiyear ice seed repository hypothesis. *J Geophys Res Biogeosci* 122. <https://doi.org/10.1002/2016JG003668>
- Palmisano AC, Sullivan CW (1983) Physiology of sea ice diatoms. II. Dark survival of three polar diatoms. *Can J Microbiol* 29:157-60
- Renaud P, Løkken T, Jørgensen L, Berge J, Johnson B (2015) Macroalgal detritus and food-web subsidies along an Arctic fjord depth-gradient. *Frontiers in Marine Science* 2:1-15. doi.org/10.3389/fmars.2015.00031
- Riedel A, Michel C, Gosselin M, LeBlanch B (2008) Winter-spring dynamics of sea-ice carbon cycling in the coastal Arctic Ocean. *J Mar Syst* 74:918-932. doi.org/10.1016/j.jmarsys.2008.01.003
- Rowan KS (1989) Photosynthetic pigments of algae. Cambridge University Press, Cambridge
- Rózanska M, Poulin M, Gosselin M (2008) Protist entrapment in newly formed sea ice in the Coastal Arctic Ocean. *J Mar Syst* 74:887-901
- Sakshaug E (2004) Primary and Secondary Production in the Arctic Seas. In: Stein R, MacDonald RW (eds) *The Organic Carbon Cycle in the Arctic Ocean*. Springer, Berlin, Heidelberg. doi.org/10.1007/978-3-642-18912-8_3
- Sakshaug E, Johnsen G, Kovacs K [eds] (2009) *Ecosystem Barents Sea*. Tapir Academic Press. Trondheim, Norway. 587 pp. ISBN 978-82-519-2461-0
- Schaub I, Wagner H, Graeve M, Karsten U (2017) Effects of prolonged darkness and temperature on the lipid metabolism in the benthic diatom *Navicula perminuta* from the Arctic Adventfjorden, Svalbard. *Polar Biol* 40:1425-1439. DOI 10.1007/s00300-016-2067-y
- Scheschonk L, Becker S, Hehemann J-H, Diehl N, Karsten U, Bischof K (2019) Arctic kelp eco-physiology during the polar night in the face of global warming: a crucial role of laminarin. *Mar Ecol Prog Ser* 611:59-74. <https://doi.org/10.3354/meps12860>
- Scholz B, Einarsson H (2015) Microphytobenthic community composition of two sub-Arctic intertidal flats in Huna Bay (Northern Iceland). *Eur J Phycol* 50:182-206. doi.org/10.1080/09670262.2015.1024286

- Seuthe L, Iversen KR, Narcy F (2011) Microbial processes in a high-latitude fjord (Kongsfjorden, Svalbard): ciliates and dinoflagellates. *Polar Biol.* 34:751–766. doi: 10.1007/s00300-010-0930-9
- Shuntanova N, Nikishina D, Ivanov M, Berge J, Renaud PE, Ivanova T, Granovitch A (2018) The longer the better: the effect of substrate on sessile biota in Arctic kelp forest. *Polar Biol* <https://doi.org/10.1007/s00300-018-2263-z>
- Smola ZT, Tatarek A, Wiktor JM, Jr JMWW, Kubiszyn A, Weslawski JM (2015) Primary producers and production in Hornsund and Kongsfjorden – comparison of two fjord systems *Polish Polar Res* 38:351-373
- Stoecker DK, Lavrentyev PJ (2018) Mixotrophic Plankton in the Polar Seas: A Pan-Arctic Review. *Front Mar Sci* 5:292. doi: 10.3389/fmars.2018.00292
- Syvrtsen, EE (1991) Ice algae in the Barents Sea: types of assemblages, origin, fate and role in the ice-edge phytoplankton bloom. *Polar Res* 10:277-288
- Vader A, Marquardt M, Meshram AR, Gabrielsen TM (2015) Key Arctic phototrophs are widespread in the polar night. *Polar Biol.* 38:13–21
- Valle KC (2005) Detection of monthly variation in marine red, brown and green macroalgae by means of in situ video technique, epifluorescence microscopy and numerical digital image analysis. Cand Scient thesis, NTNU Trondheim, 168 pp
- Valle KC, Nymark M, Aamot I, Hancke K, Winge P, Andresen K, Johnsen G, Brembu T, Bones A (2014) System responses to equal doses of photosynthetically usable radiation of blue, green, and red light in the marine diatom *Phaeodactylum tricorutum*. *PlosOne.* 9. e114211. doi:10.1371/journal.pone.0114211
- Veuger B, van Oevelen D (2011) Long-term pigment dynamics and diatom survival in dark sediment. *Limnol Oceanogr* 56:1065–74
- Volent Z, Johnsen G, Sigernes F (2007) Kelp forest mapping by use of airborne hyperspectral imager. *J App Remote Sens* 1:011503. doi:10.1117/1.2822611
- Werner I, Ikävalko J, Schünemann H (2007) Sea-ice algae in Arctic pack ice during late winter. *Polar Biol* 30:1493-1504. doi.org/10.1007/s00300-007-0310
- Weslawski JM, Wiktor J, Zajaczkowski M, Swerpel S (1993) Intertidal zone of Svalbard. *Polar Biol* 13:73-79
- Weslawski JM, Kendall MA, Wlodarska-Kowalczyk M, Iken K, Kedra M, Legezynska J, Sejr MK (2011) Climate change effects on Arctic fjord and coastal macrobenthic diversity- observations and predictions. *Mar Biodiv* 41:71–85
- Wessels H, Hagen W, Molis M, Wiencke C, Karsten U (2006) Intra- and interspecific differences in palatability of Arctic macroalgae from Kongsfjorden (Spitsbergen) for two benthic sympatric invertebrates. *J Exp Mar Biol Ecol.* 329:20-33. doi:10.1016/j.jembe.2005.08.006
- Wiencke C (1988) Notes on the development of some benthic marine macroalgae of King George Island (Antarctica). *Ser Cient INACH* 37:23–47
- Wiencke C (1990) Seasonality of brown macroalgae from Antarctica – a long-term culture study under fluctuating Antarctic daylengths. *Polar Biol* 10:589–600
- Wiencke C, Clayton MN (2002) Antarctic seaweeds. *Synopses of the Antarctic Benthos* (Wägele JW, Sieg J (eds), vol 9. Gantner, Ruggell
- Wiencke C, Clayton MN, Gomez I, Iken K, Lüder UH, Amsler CD, Karsten U, Hanelt D, Bischof K, Dunton K (2007) Life strategy, ecophysiology and ecology of seaweed in polar waters. *Rev Environ Biotechnol.* 6:95-126. DOI 10.1007/s11157-006-9106-z
- Wiencke C. (ed.) 2011. *Biology of polar benthic algae.* Marine and Freshwater Botany. Walter de Gruyter GmbH & Co. KG, New York 342 pp
- Wilce RT (1994) The Arctic subtidal as habitat for macrophytes. In: Lobban CS, Harrison PJ (eds) *Seaweed ecology and physiology.* Cambridge University Press, Cambridge, pp 89–92

- Woelfel J, Schumann R, Peine F, Flohr A, Kruss A, Tegowski J, Blondel P, Wiencke C, Karsten U (2010) Microphytobenthos of Arctic Kongsfjorden (Svalbard, Norway): biomass and potential primary production along the shore line. *Polar Biol* 33:1239-1253. doi.org/10.1007/s00300-010-0813-0
- Womersley HBS (1991) Biogeography of Australasian marine macroalgae. In: Clayton MN, King RJ (eds) *Biology of marine plants*. Longman Cheshire, Melbourne, pp 367–381.
- Zhang Q, Gradinger R, Spindler M (1998) Dark survival of marine microalgae in the high Arctic (Greenland Sea). *Polarforschung* 65:111–116